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NEW SPECIES OF PIPER FROM CENTRAL AMERICA[1]

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Piper reptabundum, n.sp.—Ramulis glabris; foliis brevissime petiolatis glabris, limbo oblique oblongo inaequilatero, basi inaequilatera altero latere rotundato altero obtuso apice longe acuminato, nervo centrali alte ultra medium nervos adscendentes utrinque 5 mittente, petiolo glabro basi ima vaginante; pedunculo glabro petiolum pluries superante filiformi; spica quam limbi dimidium multo breviore et filiformi, bracteae pelta triangulari glabra et glandulis conspersa, pedicello lato puberulo, filamentis exsertis rhachi ad basin baccae insertis, bacca libera trigona vertice glandulis conspersa, stigmatibus linearibus.

Repens vel scandens. Ramuli e nodis radicantes circiter 1.5 mm. crassi, collenchyma continuum libriforme, fasciculi intramedullares 1-seriati pauci. Limbi in sicco membranacei pellucido-punctulati usque ad 14.5 cm. longi, in medio a nervo centrali altero latere usque ad 2 cm. altero usque ad 3 cm. lati. Petioli usque ad limbi latus longius vix 2 mm., inter latera 2 mm. longi. Pedunculi fere 5 mm. longi. Stamina 3. Stigmata 3 sessilia.

COSTA RICA: Forêts de Shirores, Talamanca, alt. 1000 m., *H. Pittier* 9277.

Piper purulhanum, n.sp.—Ramulis glabris; foliis modice petiolatis glabris, limbo ovato-acuminato basi ima aequilatera

[1] The descriptions of new species presented herewith are taken from an extended manuscript account of the Panamanian and Central American species of *Piper* prepared by the late CASIMIR DE CANDOLLE, largely upon material in the U.S. National Herbarium, the Central American specimens having been included in material sent to M. DE CANDOLLE for elaboration in connection with his study of the Piperaceae collected during the recent biological survey of Panama under the auspices of the Smithsonian Institution.—WILLIAM R. MAXON, U.S. National Museum.

acuto apice obtusiuscule acuminato, nervo centrali nervos adscendentes utrinque 2 quorum supremus a 2–3 cm. supra basin solutus nervulosque validos 2–3 adscendentes mittente, nervo laterali adscendente utrinque a basi soluto, petiolo basi ima vaginante; pedunculo glabro quam petiolus breviore, spica quam limbus paullo breviore apice acuta, rhachi hirsuta, bractea spathulata apice triangulari cucullata et glabra inferne margine hirsuta, antheris oblong-ellipticis quam filamenta oblonga paullo brevioribus, ovario libero glabro, stigmatibus linearibus.

Ramuli spiciferi 2.5 mm. crassi, collenchyma fere continuum libriforme, fasciculi intramedullares 1-seriati, cellulae sclerosae in cortice circa collenchyma crebrae, canalis lysigenus unicus centralis. Limbi in sicco firmi minute pellucido-punctulati usque ad 17 cm. longi et 10.5 cm. lati. Petioli 25 mm., pedunculi 8 mm. longi. Spicae florentes 14 cm. longae et 3.5 mm. crassae, canali lysigeno centrali munitae. Stamina 3 rhachi ad basin ovarii inserta, antherae paullo sub 1 mm. longae. Stigmata 3 sessilia.

GUATEMALA: Dept. Baja Verapaz, forest near Purulhá, alt. 1800 m., *H. von Türckheim* II. 1705.

Piper tenuispicum, n.sp.—Ramulis glabris; foliis brevissime petiolatis glabris, limbo elliptico-oblongo basi subaequilatera acuto apice longe acuminato acumine mucronulato, nervo centrali nervos adscendentes alternos utrinque 4 mittente quorum supremus a 3.5 cm. supra basin solutus, petiolo basi ima vaginante; pedunculo glabro petiolum aequante, spica florente quam limbus fere $\frac{1}{3}$ breviore tenui, rhachi hirsuta, bracteae pelta triangulari glabra pedicello latiusculo hirsuto, antheris subrotundis apice apiculatis, bacca puberula.

Ramuli spiciferi vix 1.5 mm. crassi; collenchyma libriforme in fasciculos directos dispositum, fasciculi intramedullares circiter 18, 1-seriati, canalis lysigenus nullus. Limbi in sicco firmo-membranacei minute pellucido-punctulati et virescentes, usque ad 12 cm. longi et 4 cm. lati. Petioli 5 mm. longi. Spicae florentes in sicco fuscescentes fere 1 mm. crassae. Stamina 3, filamenta rhachi inserta; bacca subtetragona, stigmata 3 sessilia.

COSTA RICA: Forêts de Las Vueltas, Tucurrique, alt. 700–800 m., *H. Pittier* 13187. In field, Juan Viñas, Reventazón Valley, alt. 1000 m., *O. F. Cook* and *C. B. Doyle* 294, 295.

Piper zentanum, n.sp.—Ramulis glabris; foliis modice petiolatis glabris; limbo ovato-elliptico basi aequilatera acuto apice acute acuminato, nervo centrali usque ad $\frac{1}{2}$ longitudinis suae nervos

adscendentes utrinque 4 mittente, nervo laterali adscendente utrinque a basi soluto, petiolo basi vaginante; pedunculo glabro quam petiolus paullo breviore, spica florente limbi dimidium aequante apice acuta, bracteae apice truncato-peltatae vertice triangulari glabro pedicello angusto dorso hirsuto, antheris rotundatis parvis, bacca obpyramidato-trigona glabra, stigmatibus linearibus brevibus.

Ramuli spiciferi 2 mm. crassi, collenchyma continuum zona interna libriforme, fasciculi intramedullares 1-seriati, canalis lysigenus centralis unicus. Limbi in sicco rigido-membranacei creberrime et minute pellucido-punctulati, usque ad 18 cm. longi et 10 cm. lati, nervuli primarii transverse paralleli. Petioli usque ad 20 mm., pedunculi 18 mm. longi. Spica florens usque ad 3 mm. crassa. Stamina 3. Stigmata 3 sessilia.

COSTA RICA: Hacienda de Zent, *A. Tonduz* 14649.

PIPER AEQUALE Vahl, ϵ **elliptico-lanceolatum**, n.var.—Limbo elliptico-lanceolato basi aequilatera acuto apice longius acuminato, usque ad 13 cm. longo et 7 cm. lato.

COSTA RICA: Collines de Piedades, près San Ramón, dans une haie de *Bromelia* et sur des troncs, *H. Pittier* 14185, 14186. Collines de Chirripó, alt. 1000 m., *A. Tonduz* 14655. Buissons et bords des chemins à Nicoya, *Tonduz* 13962. Forest at Matambu, Nicoya Peninsula, alt. 600 m., *O. F. Cook* and *C. B. Doyle*.

COLOMBIA: Santa Marta, *H. H. Smith* 385.

Piper minutantherum, n.sp.—Ramulis glabris minute verruculosis; foliis modice petiolatis glabris, limbo elliptico-lanceolato basi leviter inaequilatera utrinque acuto apice subacute et sat longe acuminato, nervo centrali nervos adscendentes altero latere 4 altero 5 mittente, quorum infimus a basi supremusque fere ex $\frac{1}{2}$ longitudinis soluti, nervulo marginali a basi fere ad apicem ducto, petiolo basi ima vaginante; pedunculo glabro quam petiolus breviore, spica matura limbi dimidium aequante apice breviter acuta, rhachi glabra, bracteae pelta triangulari margine pedicelloque angusto hirtellis, antheris minutis quam filamenta tenuia multo brevioribus, bacca obovata glabra superne in stilum oblongum sat longe producta, stigmatibus minutissimis.

Ramuli spiciferi 2 mm. crassi, collenchyma in fasciculos discretos dispositum zona interna libriforme, fasciculi intramedullares 1-seriati, canalis

lysigenus unicus centralis. Limbi in sicco membranacei minute pellucido-punctulati, usque ad 21 cm. longi et 7.7 cm. lati. Petioli usque ad limbi latus longius 2.2 mm., inter limbi latera 2 mm. longi. Pedunculi 1.3 mm. longi. Spica 10 cm. longa, fere 4 mm. crassa. Stamina 3; bacca cum stilo 1.5 mm. longa.

GUATEMALA: In forest near Cubilquitz, *H. von Türckheim* II. 1441.

PIPER PELTAPHYLLUM C. DC., var. **lasvueltasanum,** n.var.—Limbo apice longe acuminato acumine obtusiusculo, bracteae pelta pedicelloque margine parce hirtellis.

COSTA RICA: Forêts de Las Vueltas, Tucurrique, alt. 635–900 m., *H. Pittier* 13189.

Piper grandilimbum, n.sp.—Ramulis glabris; foliis longe petiolatis magnis, limbo a circiter $\frac{1}{16}$ longitudinis peltato ovato-acuminato basi aequilatera haud profunde cordato apice longe et acute acuminato, supra glabro subtus ad nervos dense velutino-hirtello, 13-plinervio nervo centrali nervos adscendentes 3, quorum supremus fere ex 5 cm. supra basin solutus et sursum nervos validos utrinque mittente nervisque lateralibus utrinque 3 a petiolo divaricantibus, petiolo hirtello basi vaginante; pedunculo juniore hirtello dein glabro quam petiolus pluries breviore, spica submatura limbi dimidium superante, bracteae vertice subpeltato-triangulari margine hirtello pedicello angusto longius hirsuto, antheris globosis quam filamenta multo brevioribus, bacca glabra.

Frutex altus. Ramuli spiciferi 5 mm. crassi, collenchyma libriforme in fasciculos discretos dispositum, fasciculi intramedullares 2-seriati, canalis lysigenus unicus centralis. Limbi in sicco subrigidi minute et inconspicue pellucido-punctulati, superi usque ad 24 cm. longi et 13 cm. lati, inferi usque ad 29 cm. longi et 20 cm. lati. Petioli superi adulti 6.5 cm. longi, inferi alte supra basin vaginantes et usque ad 9 cm. longi. Pedunculus 2 cm. longus. Spica submatura in specimine viso incompleta 16 cm. longa et usque ad 4 mm. crassa canali lysigeno centrali munita. Stamina 3; bacca obpyramidato-trigona. Stigmata 3 sessilia cito decidua.—Species *P. peltaphyllo* proxima antheris rotundatis et minoribus, nervulis validis, collenchymate haud continuo ab illo discrepans.

GUATEMALA: Depart. Alta Verapaz prope Cubilquitz, alt. 350 m., in silva, *H. von Türckheim* II. 1490.

Piper pubinerve, n.sp.—Ramulis glabris; foliis modice petiolatis, limbo elliptico basi ima leviter inaequilatera acuto subacutove apice breviter acuminato, supra glabro subtus ad nervos minute

velutino, nervo centrali ex ultra ½ longitudinis suae nervos adscendentes subrectos utrinque 7 mittente, petiolo usque ad limbum vaginante; pedunculo quam petiolus paullo breviore, spica quam limbus pluries breviore apice obtusa, bracteae inferne latae vertice truncato-peltato lunulato dense puberulo, antheris parvis rotundatoovatis, ovario libero apice in stilum mediocrem attenuato, bacca matura subtetragona.

Ramuli spiciferi circiter 2 mm. crassi, collenchyma sparsim libriforme in fasciculos discretos dispositum, fasciculi intramedullares 1-seriati. Limbi in sicco firmi pallidi minute pellucido-punctulati, usque ad 18.5 cm. longi et 11 cm. lati. Petioli 12 mm. longi. Spicae maturae 22 mm. longae et usque ad 1 cm. crassae, in sicco atrorubescentes. Stamina 4 rhachi inserta. Stigmata 2 lateralia linearia et sat longa.—Species quoad limbi formam *P. ripicolam* C. DC. valde referens, foliorum et bractearum pube ac antheris rotundato-ovatis et brevioribus ab illo discrepans.

COSTA RICA: El General, alt. 600 m., *H. Pittier* 10607.

Piper virgultorum, n.sp.—Ramulis junioribus puberulis cito glabris et verruculosis; foliis modice petiolatis, limbo ellipticolanceolato basi inaequilatera latere longiore subacuto breviore acuto, apice longe et acute acuminato, supra glabro subtus ad nervos adpresse hirtello, nervo centrali nervos adscendentes altero latere 5 altero 4 mittente quorum supremus fere a 6 cm. supra basin solutus, petiolo primum puberulo dein glabro et verruculoso basi ima vaginante; pedunculo glabro quam petiolus paullo breviore, spica florente quam limbi dimidium paullo breviore apice mucronata, rhachi glabra, antheris rotundato-reniformibus parvis quam filamenta oblonga paullo brevioribus, ovario inferne rhachi immerso superne libero glabro ovato-acuto, stigmatibus 2 linearibus transversalibus.

Ramuli spiciferi 1.5 mm. crassi, collenchyma in fasciculos discretos dispositum et zona interna libriforme, fasciculi intramedullares 1-seriati, canalis lysigenus nullus. Limbi in sicco firme membranacei minute et inconspicue pellucido-punctulati, usque ad 18.5 cm. longi et 6.5 cm. lati. Petioli usque ad limbi latus longius 6 mm. inter limbi latera 2 mm. longi. Spicae florentes 6 cm. longae et 2 mm. crassae. Stamina 4.

COSTA RICA: Broussailles de Tsuritkub, Talamanca, alt. 100 m., *H. Pittier* 8650. Forêts sur les bords du Río Yurquin, *H. Pittier* 8570, cum spicis juvenilibus.

Piper tenuipes, n.sp.—Ramulis glabris tenuiter costulatis; foliis modice petiolatis parvis glabris, limbo ovato-lanceolato basi aequilatera acuto apice acute acuminato, petiolo basi ima vaginante; pedunculo glabro petiolum adultum subaequante tenui, spica florente quam limbus fere $\frac{1}{3}$ breviore tenui sublaxiflora, rhachi hirsuta, antheris reniformibus quam filamenta paullo brevioribus, ovario glabro ad rhachim elongato, stigmatibus ovatis obtusis.

Frutex 2–3 m. altus. Ramuli spiciferi 0.5 mm. crassi, collenchyma in fasciculos discretos dispositum haud libriforme, fasciculi intramedullares 1-seriati, canalis lysigenus nullus. Limbi in sicco membranacei minute pellucido-punctulati, superi usque ad 7.5 cm. longi et 3.1 cm. lati. Petioli 7 mm., pedunculi circiter 6 mm. longi. Spicae florentes 3.6 cm. longae et 0.5 mm. crassae. Stamina 4. Stigmata 3 vel rarius 4.

COSTA RICA: Bois clairs et humides des collines de Piedades près San Ramón, alt. 1100 m., *A. Brenes* 14193. Lisière des bois humides au Cerro San Isidoro, près San Ramón, alt. 1300 m., *Brenes* 14196.

Piper cubilquitzianum, n.sp.—Ramulis glabris; foliis breviter petiolatis glabris, limbo elliptico-lanceolato basi aequilatera acuto apice longe et obtusiuscule protracto-acuminato, 5-nervio, petiolo basi ima vaginante; pedunculo glabro petiolum paullo superante, spica quam limbus paullo breviore, rhachi dense et breviter hirsuta, bractea obovata vertice inflexo nuda inferne subtus hirsuta, antheris reniformibus brevibus, baccis sublaxe dispositis ellipticis glabris, stigmatibus rotundatis.

Ramuli spiciferi 1 mm. crassi, collenchyma in fasciculos discretos lunulatos dispositum et haud libriforme, fasciculi intramedullares 1-seriati, canalis lysigenus nullus. Limbi in sicco membranacei minute pellucido-punctulati, usque ad 12 cm. longi et 5 cm. lati. Petioli 5 mm., pedunculi 7 mm. longi. Stamina 4 rhachi inserta, bacca paullo sub 1 mm. longa.

GUATEMALA: Forests near Cubilquitz, Depart. Alta Verapaz, *H. von Türckheim* II. 1440.

Piper nicoyanum, n.sp.—Ramulis junioribus puberulis cito glabris; foliis modice petiolatis, limbo supra glabro subtus ad nervos hirtello, 7-nervio, petiolo hirtello basi vaginante; pedunculo juniore puberulo longitudine variabili quam petiolus breviore vel longiore, spica matura limbum paullo superante, rhachi hirsuta, bractea rotundata basi extus hirsuta, antheris reniformibus filamenta superantibus, ovario libero apice disculum orbiculare in

medio stigmatiferum gerente, stigmatibus ovatis, baccis fere globosis glabris.

Ramuli spiciferi 1 mm. crassi, collenchyma haud libriforme, in fasciculos discretos dispositum, fasciculi intramedullares 1-seriati, canalis lysigenus unicus centralis. Limbi in sicco membranacei crebre pellucido-punctulati, superi usque ad 8 cm. longi et 7 cm. lati. Petioli superi usque ad 1.5 cm. longi. Spicae maturae circiter 9 cm. longae. Stamina 4 basi ima baccae adnata, bacca circiter 1.5 mm. crassa. Stigmata 3–4, sessilia.—Vern. *alcotán*.

COSTA RICA: Bords des chemins à Nicoya, *H. Pittier* 13689, 13696.

Piper bryogetum, n.sp.—Ramulis glabris; foliis brevissime petiolatis glabris, limbo ovato-elliptico basi aequilatera rotundato apice acute acuminato, nervo centrali nervos adscendentes utrinque 2 mittente quorum supremus fere ex $\frac{1}{3}$ longitudinis centralis solutus, nervis lateralibus adscendentibus utrinque 2 a basi solutis, petiolo basi ima vaginante; pedunculo glabro petiolum aequante, spica matura quam limbi dimidium paullo breviore apice attenuata, bracteae pelta triangulari margine aureo-hirsuta pedicello angusto hirtello, bacca glabra vertice flavide glandulosa.

Frutex ad truncos muscosos scandens. Ramuli spiciferi fere 1 mm. crassi, collenchyma tenue continuum libriforme, fasciculi intramedullares 1-seriati, canalis lysigenus nullus. Limbi in sicco membranacei pellucido-punctulati, circiter 13 cm. longi et 6 cm. lati. Petioli fere 10 mm. longi. Spica matura 3 mm. crassa. Stamina 4 ad basin baccae rhachi inserta, bacca obpyramidato-trigona. Stigmata 3 sessilia.

COSTA RICA: Forêts de Las Vueltas, Tucurrique, alt. 635 m., *H. Pittier* 12939. Le long du Río Hondo, plaines de Santa Clara, alt. 100 m., *O. F. Cook* and *C. B. Doyle* 563. Hacienda de Zent, alt. 30 m., *H. Pittier* 14652.

Piper longistipulum, n.sp.—Foliis breviter petiolatis subobovato-ellipticis, basi leviter inaequilatera utrinque rotundato-cordulatis, apice oblique et sat longe acuminatis, utrinque glabris, nervo centrali usque ad $\frac{1}{2}$ longitudinis suae nervos adscendentes alternos 4 et e basi 2–3 tenuiores utrinque mittente quorum infimi magis divaricantes; petiolo glabro basi vaginante, stipulis longis apice filiformibus; pedunculo glabro petiolum totum paullo superante; spica per anthesin limbi dimidium aequante apice sterili acuta, bracteae glabrae vertice triangulari inflexo, pedicello aequilato supra canaliculato.

Ramuli glabri, spiciferi 2 mm. crassi, collenchyma in fasciculos discretos dispositum et zona interna libriforme, fasciculi intramedullares 1-seriati,

canalis lysigenus nullus. Limbi in sicco membranacei pellucido-punctulati, 20 cm. longi, 7.5 cm. lati. Petioli usque ad limbi latus majus fere 8 mm., inter limbi latera 3 mm. longi. Stipulae membranaceae circiter 30 mm. longae. Spica per anthesin 8 cm. longa, fere 3 mm. crassa, in vivo atro-rubescens. Stamina 4, antherae subglobosae quam filamenta breviores. Bacca nondum matura tetragona lateraliter compressa. Stigmata 3 sessilia brevia.

COSTA RICA: Forêts du Río Naranja, alt. 200–250 m., *H. Pittier* 8001.

Piper melanocladum, n.sp.—Ramulis glabris in sicco nigris; foliis modice petiolatis glabris, limbo ovato-oblongo basi leviter inaequilatera altero latere rotundato altero acuto superne sat longe acuminato et apice obtusiusculo, nervo centrali nervos adscendentes utrinque 3 mittente quorum supremus paullo supra medium centralis solutus, nervis lateralibus adscendentibus altero latere 1 altero 2 a basi solutis, petiolo usque ad limbum vaginante; pedunculo glabro petiolum aequante, spica fere matura limbi dimidium paullo superante apice mucronulata, bracteae fere glabrae vertice triangulari et carnoso peltam simulante et margine infero puberulo, parte infero lata cucullata et glabra, antheris ovatis quam filamenta exserta multo brevioribus, bacca rotundato-subtetragona libera, stigmatibus oblongis apice acutis.

Ramuli spiciferi 2 mm. crassi, collenchyma in fasciculos discretos et sat crassos dispositum haud libriforme et cellulis brunneis intermixtum, fasciculi intramedullares 2-seriati. Limbi in sicco coriacei, superi usque ad 23 cm. longi et 7.5 cm. lati, subsequentes basi aequilatera rotundati usque ad 25 cm. longi et 9 cm. lati. Petioli usque ad limbi latus longius circiter 2 cm. et inter limbi latera 3 mm. longi. Spica in sicco nigra, bracteae coriaceae. Stamina 4, basi ima baccae adnata. Stigmata 3 sessilia.

COSTA RICA: Bords de l'Ariei, Talamanca, *H. Pittier* 9390. Forêts de Las Vueltas, Tucurrique, alt. 635–700 m., *Pittier* 13148.

Piper pallidifolium, n.sp.—Ramulis adpresse hirtellis; foliis brevissime petiolatis, limbo oblongo-elliptico-lanceolato basi leviter inaequilatera cordulato apice sat longe et acute acuminato, supra glabro subtus praesertim ad nervos nervulosque adpresse pilosulo, nervo centrali nervos adscendentes utrinque 3 quorum supremus fere ex $\frac{1}{2}$ longitudinis solutus, sursumque nervulos validos fere tota longitudine mittente, nervis lateralibus utrinque 2–3 a basi divaricantibus, petiolo hirsuto basi vaginante; pedunculo puberulo juvenili quam petiolus paullo breviore, spica subflorente quam limbus pluries breviore apice mucronata mucrone filiformi, bracteae

breviter spathulatae punctis rubellis notatae vertice inflexo margine infero puberulo, antheris ovatis.

Ramuli spiciferi 1 mm. crassi, collenchyma partim libriforme in fasciculos discretos dispositum, fasciculi intramedullares 1-seriati, canalis lysigenus nullus cellulis rubris in medulla crebris. Limbi in sicco membranacei cinerascentes rubello-pellucido-punctulati usque ad 12 cm. longi et fere usque ad 2.6 cm. lati. Petioli usque ad limbi latus longius 4 mm. inter limbi latera 2 mm. longi. Spicae in specimine adhuc juveniles 1.5 cm. longae et 1.5 mm. crassae. Stamina 4. Ovarium nondum formatum.

COSTA RICA: Bords de l'Ariei, Talamanca, *H. Pittier* 9392.

Piper pansamalanum, n.sp.—Ramulis hirtellis; foliis sat longe petiolatis, limbo ovato basi modice inaequilatera cordato lobis rotundatis apice breviter attenuato-acuto, supra glabro subtus ad nervos nervulosque hirsuto, nervo centrali nervos adscendentes utrinque 3 mittente quorum supremus fere ex ½ longitudinis centralis solutus, nervis lateralibus utrinque 3 a basi divaricantibus, petiolo hirtello usque ad limbum vaginante; pedunculo glabro quam petiolus paullo breviore, spica limbum superante crassa apice attenuata, bracteae vertice inflexo-peltato triangulari margine hirsuto pedicello aequilato dorso hirsuto, antheris rotundatis quam filamenta multo brevioribus, bacca libera glabra tetragona, stigmatibus linearibus.

Ramuli spiciferi circiter 4 mm. crassi, collenchyma in fasciculos discretos crassos et confertos dispositum, non libriforme, fasciculi intramedullares 2-seriati. Limbi in sicco subcoriacei usque ad 26 cm. longi et 20 cm. lati, lobi basilares usque ad 5.5 cm. longi ad petiolum aequilongi. Petioli circiter 4 cm., pedunculi usque ad 5.5 cm. longi. Spica matura 40 cm. longa et usque ad 9 mm. crassa. Stamina 4 basi ima baccae adnata, antherae 0.5 mm. longae, stigmata 3 sessilia.

GUATEMALA: Pansamalá, Depart. Alta Verapaz, alt. 1140 m., *H. von Türckheim* 940. Silva supra Panzal, alt. 1200 m., *von Türckheim* II. 1703.

Piper magnilimbum, n.sp.—Ramulis glabris; foliis modice petiolatis, limbo elliptico basi valde inaequilatera cordato apice acute attenuato, supra glabro subtus ad nervos nervulosque puberulo, nervo centrali subtus squamis oblongis instructo nervos adscendentes utrinque 4–5 mittente quorum supremus paullo supra ½ longitudinis solutus, nervis lateralibus utrinque 3–4 a basi divaricantibus, petiolo subtus squamis oblongis instructo et puberulo, usque ad limbi latus longius vaginante; pedunculo

minute puberulo petiolum fere aequante, spica limbum aequante, bracteae obovato-oblongae dorso puberulae vertice lanulato nudo et calloso, ovario libero glabro apice attenuato.

Collenchyma fere continuum zona interna libriforme, fasciculi intramedullares 3-seriati, canalis lysigenus nullus. Limbi in sicco firmi opaci, circiter 36 cm. longi et 26 cm. lati, lobi basilares rotundati discreti quorum major 10 cm. longus petiolum velans. Petioli usque ad limbi latus longius 7 cm., inter limbi latera 1–1.5 cm. longi. Spica post anthesin 6 mm. crassa apice acuta. Stamina 4 basi ovario adnata, stigmata 3 minuta sessilia et cito decidua.

COSTA RICA: Cañas Gordas, alt. 1100 m., *H. Pittier* 11032, 11073.

Piper euryphyllum, n.sp.—Ramulis glabris; foliis modice petiolatis, limbo ample ovato basi inaequilatero lateribus sat inaequilongis et parum inaequilatis, apice acuminato, supra glabro subtus ad nervos puberulo, nervo centrali nervos adscendentes utrinque 4 mittente quorum supremus paullo supra medium centralis solutus, nervis lateralibus utrinque 2 a basi solutis, petiolo subtus adpresse hirsuto usque ad limbum vaginante; pedunculo glabro quam petiolus paullo breviore, spica folium superante, bracteae cucullatae extus hirsutae intus glabrae vertice triangulari puberulo, ovario libero glabro, stigmatibus linearibus.

Ramuli spiciferi 5 mm. crassi, collenchyma in fasciculos discretos dispositum haud libriforme, cellulis fuscis intermixtum, fasciculi intramedullares 3-seriati. Limbi in sicco firmi fuscescentes pellucido-punctulati, usque ad 31 cm. longi et 21 cm. lati. Petioli circiter 5.5 cm. longi. Spica florens fere usque ad 1 cm. crassa. Stamina 4 basi ovarii adnata; bacca adulta verisimiliter tetragona, stigmata 3, sessilia.

COSTA RICA: Forêts de la Palma, alt. 1459 m., *H. Pittier* 12666.

Piper biseriatum, n.sp.—Ramulis dense villosis; foliis modice petiolatis, limbo subovato-elliptico basi valde inaequilatera cordato lobis conniventibus majore petiolum velante auriformi, apice sat longa acuminato, supra sparsim et longe piloso, subtus ad nervum centralem longe et ad paginam brevius et dense piloso, nervo centrali nervos adscendentes utrinque 3–4 mittente quorum supremus ex $\frac{1}{2}$ longitudinis centralis solutus, nervis lateralibus utrinque altero latere 2–3 altero 4–5 a basi divaricantibus, petiolo usque ad limbi latus brevius vaginante et dorso dense villoso, stipulis glabris; pedunculo glabro quam petiolus breviore, spica florente limbum superante, bracteae pelta ovato-triangulari inferne carnosa et

margine puberula superne membranacea et margine hirsuta, pedicello aequilato parce puberulo, antheris reniformibus.

Ramuli spiciferi fere 3 mm. crassi, collenchyma in fasciculos discretos dispositum, haud libriforme, fasciculi intramedullares 2-seriati, canalis lysigenus nullus. Limbi in sicco firmi opaci crebre pellucido-punctulati cum lobo auriformi usque ad 23.5 cm. longi et 11.5 cm. lati. Petioli usque ad limbi latus longius 3–3.5 cm., inter limbi latera 0.5 cm., pedunculi usque ad 2.5 cm. longi. Spica florens circiter 3 mm. crassa. Stamina 4.

COSTA RICA: Cañas Gordas, alt. 1100 m., *H. Pittier* 11036.

Piper pilibaccum, n.sp.—Ramulis altero latere sub foliis hirsutis; foliis breviter petiolatis, limbo ovato-oblongo basi leviter inaequilatera altero latere rotundato obtusove acuto apice acute et sat longe acuminato, supra glabro subtus praesertim ad nervos et nervulos hirtello, nervo centrali nervos patule adscendentes tenues utrinque 5 mittente quorum supremus fere ex ½ longitudinis centralis solutus, petiolo subtus hirsuto fere usque ad medium vaginante; pedunculo glabro petiolum aequante, spica submatura quam limbus fere quadruplo breviore apice mucronulata, bractea obovata cucullata dorso et margine hirsuta, antheris reniformibus filamenta fere aequantibus, bacca libera trigona vertice dense hirsuta, stigmatibus subobovatis acutis.

Ramuli spiciferi 1 mm. crassi, adulti glabri, in 5 mm. crassis collenchyma continuum zona interna interrupta libriforme, fasciculi intramedullares 2-seriati, canalis lysigenus unicus centralis et tenuis. Limbi in sicco membranacei fusci minute pellucido-punctulati, usque ad 12.5 cm. longi et 4.5 cm. lati. Petioli usque ad limbi latus longius 4 mm., inter limbi latera 1.5 mm. longi. Spica submatura fere 4 cm. longa 1 mm. crassa. Stamina 4, bacca in vertice complanato rubiginose hirsuta. Stigmata 3.—Species *P. carpinteranum* C. DC. sat referens, bacca hirsuta ab illo discrepans.

COSTA RICA: In forest, Matambu, Nicoya Peninsula, alt. 600 m., *O. F. Cook* and *C. B. Doyle* 702.

PIPER SEPIUM C. DC., **β glabrum,** n.var.—Limbo utrinque glabro quam in specie longiore, usque ad 11 cm. longo et 2.5 cm. lato.

COSTA RICA: Cours supérieur du Diquís, *H. Pittier* 10570.

PIPER SEPIUM C. DC., **γ guacimonum,** n. var.—Limbo utrinque glabro et subtus nigro-punctulato, quam in specie paullo majore, foliorum superiorum usque ad 11.5 cm. longo et 4.5 cm. lato.

COSTA RICA: Hacienda de Guácimo, alt. 120 m., *A. Tonduz* 14656.

Piper nanum, n.sp.—Caule villoso inferne e nodis radicante; foliis brevissime petiolatis, limbo oblongo-ovato basi inaequilatera cordulato apice acute acuminato, utrinque et praesertim ad nervos villoso, nervo centrali nervos altero latera 4 altero 5 mittente quorum superi adscendentes, inferi subadscendentes, petiolo villoso usque ad limbi latus longius vaginante; pedunculo villoso petiolum aequante, spica juvenili petiolum paullo superante tenui apice tenuiter mucronata, bracteae cucullatae dorso hirtellae vertice inflexo nudo, antheris ovatis filamenta fere aequantibus.

Suffrutex circiter 30 cm. altus. Caulis inferne usque ad 3 mm., superne 1 mm. crassus, collenchyma in fasciculos discretos dispositum et zona interna libriforme, fasciculi intramedullares 1-seriati, canalis lysigenus nullus. Limbi in sicco membranacei minute pellucido-punctulati, usque ad 14.5 cm. longi et 4.5 cm. lati. Petioli usque ad limbi latus longius 2 mm., inter limbi latera fere 1 mm. longi. Spica juvenilis 8 mm. longa et fere 1.5 mm. crassa. Stamina 4.

COSTA RICA: In atlantica declivitate, ad Guácimo, alt. 141 m., *A. Tonduz* 14659.

Piper Brenesii, n.sp.—Ramulis glabris; foliis breviter petiolatis glabris, limbo late elliptico basi leviter inaequilatera altero latere rotundato altero acuto, apice breviter et obtusiuscule acuminato, nervo centrali nervos adscendentes oppositos utrinque 6–7 mittente quorum supremus supra $\frac{1}{2}$ longitudinis centralis solutus, petiolo usque ad limbum vaginante; pedunculo glabro quam petiolus fere duplo breviore, spica quam limbus pluries breviore crassa apice mucronata, bracteae latae glabrae vertice inflexo triangulari, bacca libera glabra vertice rhomboidali.

Frutex 1–1.5 m. altus. Ramuli spiciferi 5 mm. crassi in sicco tetragoni, collenchyma in fasciculos discretos dispositum et zona interna libriforme, fasciculi intramedullares 2-seriati. Limbi in sicco firme membranacei crebre pellucido-punctulati, 20 cm. longi 11 cm. lati. Petioli 2 cm., pedunculi 1 cm. longi. Spicae maturae 5 cm. longae et 6 mm. crassae. Stamina 4 basi ima baccae adnata. Stigmata 3, sessilia cito caduca.

COSTA RICA: Petits bois des collines de Santiago à San Ramón, *Brenes* 14190.

Piper mombachanum, n.sp.—Ramulis glabris; foliis modice petiolatis glabris, limbo oblongo-elliptico-lanceolato basi inaequilatera altero latere subrotundato altero acuto, apice acute et sat longe acuminato, nervo centrali nervos adscendentes utrinque

4–5 mittente quorum supremus fere ex ½ longitudinis centralis solutus, petiolo basi ima vaginante; pedunculo glabro petiolum paullo superante, spica matura limbi dimidium fere aequante, apice mucronulata vel obtusa, bracteae pelta triangulari fere glabra pilis aliquot brevibus in marginibus lateralibus munita, pedicello subglabro angusto, antheris reniformibus quam filamenta paullo brevioribus, bacca libera tetragona lateraliter compressa apice minute puberula, stigmatibus linearibus.

Frutex divaricato-ramosus 3–3.5 m. altus. Ramuli spiciferi 1 mm. crassi, collenchyma subcontinuum zona interna libriforme, fasciculi intramedullares 1-seriati, canalis lysigenus nullus. Limbi in sicco membranacei crebre pellucido-punctulati, 14.5–15.5 cm. longi, 4–5 cm. lati. Petioli usque ad limbi latus longius 7 mm., inter limbi latera 3 mm., pedunculi 15 mm. longi. Spica matura 8 cm. longa, 2 mm. crassa. Stamina 4 baccae alte adnata. Stigmata 3 sessilia.

NICARAGUA: Volcán Mombacho, Depart. Granada, in deep woods, *C. F. Baker* 2462.

COSTA RICA: Bois de San Pedro près San Ramón, alt. 1300–1400 m., *A. Tonduz* 17765, 17784.

Piper flaviramum, n.sp.—Ramulis parce hirtellis; foliis brevissime petiolatis glabris, limbo subovato-oblongo basi leviter inaequilatera obtuso, apice longe acuminato, nervo centrali nervos adscendentes utrinque 5 mittente quorum supremus fere a ¼ longitudinis nervi centralis solutus, petiolo basi ima vaginante; pedunculo glabro petiolum multo superante; spica juvenili quam limbus pluries breviore in sicco rubescente, bracteae pelta triangulari margine hirsuta pedicello sat angusto glabro, ovario libero ovato-acuto glabro.

Scandens, ramuli in sicco flavi, teretes, spiciferi fere 1 mm. crassi, collenchyma continuum libriforme, fasciculi intramedullares 1-seriati, canalis lysigenus nullus. Limbi in sicco firme membranacei, flavicantes, minute pellucido-punctulati, circiter 16 cm. longi et 4.5 cm. lati. Petioli fere 3 mm., pedunculi fere 7 mm. longi. Spica juvenilis 2.5 cm. longa et 1.5 mm. crassa. Stamina 4. Stigmata 3.—Species *P. xanthostachio* proxima ab illo foliis subsessilibus, ramulis hirtellis et spicarum juvenilium colore sat discrepans.

COSTA RICA: Forêts de La Palma, alt. 1450 m., *H. Pittier* 12510.

Piper gibbifolium, n.sp.—Ramulis glabris; foliis modice petiolatis, limbo elliptico-obovato basi inaequilatero, lateribus ad petiolum aequilongis valde inaequilatis altero rotundato altero

acuto, apice acuminato, supra glabro subtus ad nervos nervulosque puberulo, nervo centrali nervos altero latere 5 altero 8 mittente quorum supremus fere ex ½ longitudinis centralis solutus, petiolo glabro basi ima vaginante; pedunculo glabro; spica subflorente quam limbus pluries breviore apice subacuta, bracteae pelta triangulari margine pedicelloque angusto hirsutis, antheris ovatis.

Ramuli in sicco nigrescentes, spiciferi 2 mm. crassi, in 4 mm. crassis collenchyma in fasciculos a latere valde productos dispositum seu subcontinuum et zona interna libriforme, fasciculi intramedullares 2-seriati, canalis lysigenus unicus centralis. Limbi in sicco firme membranacei, parce pellucido-punctulati, fere 22 cm. longi et 11 cm. lati apice in specimine viso incompleti. Petioli usque ad limbi latus longius 13 mm., inter limbi latera 3 mm., pedunculi 8 mm. longi. Spica subflorens 6 cm. longa et basi 3 mm. crassa. Stamina 4.

COSTA RICA: Hacienda de Zent, alt. 31 m., *A. Tonduz* 14649 in Herb. Inst. Fís. Geogr. Costar. et Herb. Berol., non eadem planta ut eodem numero in Herb. Boiss.

Piper brachistopodum, n.sp.—Ramulis glabris; foliis brevissime petiolatis, limbo elliptico basi leviter inaequilatera altero latere rotundato altero acuto apice acute acuminato, supra glabro subtus ad nervos minute puberulo, nervo centrali nervos alternos adscendentes altero latere 4 altero 5 mittente quorum supremus ex ½ longitudinis centralis solutus, petiolo basi ima vaginante; pedunculo glabro quam petiolus breviore, spica matura limbi dimidium vix aequante apice obtusa, bracteae pelta parva triangulari margine infero hirtella pedicello glabro inferne cuneato, antheris rotundatis quam filamenta brevioribus, bacca subtetragona glabra, stigmatibus minutis.

Ramuli spiciferi circiter 3 mm. crassi, collenchyma in fasciculos discretos dispositum zona interna libriforme, fasciculi intramedullares 1-seriati. Limbi in sicco membranacei pellucido-punctulati, circiter 21 cm. longi et 9 cm. lati. Petioli usque ad limbi latus longius 5 mm., inter limbi latera 3 mm., pedunculi adulti 4 mm. longi. Spica matura 9 cm. longa, 4 mm. crassa. Stamina 4 supra medium baccae inserta. Stigmata 3 sessilia.

COSTA RICA: Forêts de Las Vueltas, Tucurrique, alt. 635–700 m., *A. Tonduz* 13143.

Piper uvitanum, n.sp.—Ramulis hirtellis; foliis brevissime petiolatis, limbo ovato-elliptico basi leviter inaequilatera utrinque obtuso, apice acute acuminato, supra glabro subtus velutino-pubescente, nervo centrali fere ex ½ longitudinis suae nervos patule

adscendentes utrinque 4–5 sursumque nervulos saepe validos mittente, petiolo hirtello basi vaginante; pedunculo hirtello petiolum subaequante, spica submatura quam limbus fere quadruplo breviore apice obtusa, bracteae vertice truncato lunulato-triangulari margine dense et fulvescente hirsuto pedicello sat lato extus hirsuto, antheris rotundatis parvis, bacca tetragona vertice dense et fulvescente hirsuta.

Ramuli spiciferi circiter 2 mm. crassi, collenchyma libriforme in fasciculos discretos a latere productos dispositum seu subcontinuum, fasciculi intramedullares 1-seriati, canalis lysigenus nullus. Limbi in sicco membranacei creberrime pellucido-punctulati, usque ad 20 cm. longi et 10 cm. lati. Petioli usque ad limbi latus longius 10 mm., inter limbi latera 3 mm. longi. Spica submatura in sicco fulvescens fere 4 mm. crassa. Stamina 4 alte cum bacca connata. Stigmata 3 sessilia.

COSTA RICA: Îlot de la Uvita, Puerto Limón, *H. Pittier* 12690.

PIPER SUBSESSILIFOLIUM C. DC., β **palmanum,** n.var.—Pilis ramulorum haud retrorsis.

COSTA RICA: Forêts de La Palma, alt. 1459 m., *H. Pittier* 12662.

Piper vestitifolium, n.sp.—Ramulis villosis; foliis breviter petiolatis, limbo oblongo-ovato-acuminato basi inaequilatera altero latere rotundato altero acuto, apice acute et sat longe acuminato, utrinque dense hirsuto, nervo centrali nervos adscendentes utrinque 5 mittente quorum supremus paullo infra medium centralis solutus, petiolo dense hirsuto basi ima vaginante; pedunculo dense hirsuto petiolum fere aequante, spica limbi dimidium subaequante apice acuta, bracteae pelta triangulari margine pedicelloque angusto hirsutis, antheris rotundatis parvis quam filamenta oblonga brevioribus, bacca subtetragona apice parce pilosula, stigmatibus linearibus brevissimis.

Ramuli spiciferi 1.5 mm. crassi, in 3 mm. crassis collenchyma in fasciculos discretos dispositum, fasciculi intramedullares 1-seriati, canalis lysigenus nullus. Limbi in sicco membranacei minute pellucido-punctulati, 10.5 cm. longi, 4 cm. lati. Petioli usque ad limbi latus longius 2 mm., inter limbi latera 3 mm., pedunculi 6 mm. longi. Spica submatura 6 cm. longa usque ad 3 mm. crassa. Stamina 4 basi baccae adnata, stigmata 3 sessilia.

GUATEMALA: Near the Finca Sepacuité, Alta Verapaz, *O. F. Cook* and *R. F. Griggs* 651.

Piper perhispidum, n.sp.—Ramulis dense hirsutis pilis sat longis; foliis breviter petiolatis, limbo oblongo-ovato-acuminato

basi inaequilatera utrinque rotundato, apice acute et sat longe acuminato, utrinque sat longe hirsuto, adulto supra scabro et bullato, nervo centrali nervos adscendentes utrinque 5 mittente quorum supremus paullo infra medium solutus, petiolo dense hirsuto basi ima vaginante; pedunculo hirsuto petiolum fere aequante, spica matura limbi dimidium paullo superante apice obtuse mucronata mucrone hirsuto, bracteae pelta triangulari margine pedicelloque angusto hirsutis, antheris reniformibus, bacca tetragona lateraliter compressa apice dense hirtella, stigmatibus linearibus.

Ramuli spiciferi 2.5 mm. crassi pilis 1.5 mm. longis; collenchyma continuum zona interna libriforme, fasciculi intramedullares partim 2-seriati, canalis lysigenus nullus. Limbi in sicco rigidi creberrime pellucido-punctulati, usque ad 17 cm. longi et ad 7 cm. lati. Petioli usque ad limbi latus longius 5 mm., inter limbi latera 3 mm. longi. Spicae maturae 7.5 cm. longae et usque ad 2.5 mm. crassae in sicco fuscescentes. Stamina 4 baccae supra basin adnata. Stigmata 3 sessilia.

COSTA RICA: Bords du Río Barranca, près San Juan de San Ramón, alt. 1500–1600 m., *A. Tonduz* 17771.

Piper submultiplinerve, n.sp.—Ramulis glabris; foliis longiuscule petiolatis glabris, limbo oblongo-ovato basi leviter inaequilatera utrinque acuto, apice acute acuminato, nervo centrali nervos adscendentes altero latere 4 altero 5 mittente, quorum supremus ex $\frac{1}{3}$ longitudinis centralis solutus et infimus basi proximus, petiolo ultra medium vaginante; pedunculo puberulo quam petiolus multo breviore, spica florente quam limbus fere triplo breviore apice acuta, bracteae pelta lunulata margine pedicelloque aequilato flavo-hirsutis, antheris exsertis ovatis quam filamenta multo brevioribus, ovario glabro apice attenuato.

Ramuli spiciferi 2 mm. crassi verruculis concoloribus asperati, collenchyma continuum zona interna libriforme, fasciculi intramedullares 1-seriati, canales lysigeni 2 in medulla. Limbi in sicco membranacei crebre pellucido-punctulati, fere usque ad 15.5 cm. longi et 7 cm. lati. Petioli usque ad limbi latus longius 30 mm., inter limbi latera 3 mm. longi. Stamina 4, stigmata 3.

COSTA RICA: Vallée de Los Orcángeles, massif de Iscazú, alt. 1700 m., *H. Pittier* 13626.

Piper leptoneuron, n.sp.—Ramulis glabris; foliis modice petiolatis glabris, limbo elliptico-lanceolato basi aequilatera acuto,

apice acute acuminato, nervo centrali nervos adscendentes tenues utrinque 4 mittente quorum supremus fere e medio centralis solutus, petiolo basi ima vaginante; pedunculo glabro petiolum aequante, spica juvenili quam limbus fere quadruplo breviore, bracteae vertice truncato margine pedicelloque hirsutis.

Ramuli laeves, spiciferi 1 mm. crassi, collenchyma continuum zona interna partim libriforme, fasciculi intramedullares 2-seriati. Limbi in sicco membranacei opaci parce pellucido-punctulati, 8.5–9 cm. longi, 3–4 cm. lati, acumen 10 mm. longum. Petioli circiter 10 mm longi. Spica in specimine adhuc juvenilis 1.5 mm. crassa. Stamina 4. .

COSTA RICA: Santa Clara, Las Delicias, alt. 500 m., *H. Pittier* 10675.

Piper nodosum, n.sp.—Ramulis glabris; foliis brevissime petiolatis, limbo elliptico-lanceolato basi levissime inaequilatera utrinque acuto, apice acuminato, supra glabro subtus ad nervos minutissime puberulo, nervo centrali nervos adscendentes sat tenues utrinque 5 mittente quorum supremus e medio centralis solutus, petiolo glabro basi ima vaginante, pedunculo glabro petiolum aequante, spica limbi dimidium superante; bracteae apice truncatae vertice triangulari margine antico minute puberulo pedicello dorso parce hirtello, antheris minutis quam filamenta multo brevioribus, bacca glabra tetragona.

Ramuli laeves in sicco pallidi, spiciferi 1.5 mm. crassi, collenchyma in fasciculos discretos dispositum et zona interna libriforme, fasciculi intramedullares 1-seriati. Limbi in sicco membranacei crebre pellucido-punctulati, usque ad 16 cm. longi et 6 cm. lati. Petioli vix 5 mm. longi. Spica matura circiter 11 cm. longa et usque ad 4 mm. crassa apice obtusa. Stamina 4 basi ima baccae adnata. Stigmata 3 sessilia.

COSTA RICA: Cañas Gordas, alt. 1100 m., *H. Pittier* 11072.

Piper diquisanum, n.sp.—Ramulis glabris verruculis asperatis; foliis breviter petiolatis glabris, limbo oblongo-ovato-lanceolato basi parum inaequilatera utrinque acuto, apice longe et acute acuminato, nervo centrali nervos adscendentes utrinque 5 mittente quorum supremus fere a medio centralis solutus petiolo basi ima vaginante; pedunculo glabro petiolum duplo superante, spica florente limbi dimidium fere aequante apice obtusa, bracteae pelta triangulari parva margine minute puberula pedicello angusto antheris ovato-rotundis filamenta fere aequantibus, ovario glabro, stigmatibus linearibus.

Ramuli spiciferi vix 2 mm. crassi, collenchyma subcontinuum zona interna libriforme, fasciculi intramedullares 1-seriati, canalis lysigenus nullus. Limbi in sicco membranacei crebre pellucido-punctulati fere 15 cm. longi et 4 cm. lati. Petioli usque ad limbi latus longius 7 mm., inter limbi latera circiter 8.5 mm., pedunculi fere 22 mm. longi. Spicae florentes circuiter 8.5 cm. longae et 3 mm. crassae. Stamina 4. Stigmata 3 sessilia.

COSTA RICA: Cours supérieur du Diquís, *H. Pittier* 10567.

Piper chirripoense, n.sp.—Ramulis glabris; foliis breviter petiolatis, limbo elliptico-lanceolato basi leviter inaequilatera utrinque acuto, apice acute et longiuscule acuminato, supra remote piloso subtus ad nervos dense piloso et ad paginam puberulo, nervo centrali nervos adscendentes utrinque 7 mittente quorum supremus supra medium centralis solutus, petiolo subtus dense piloso usque ad limbum vaginante; pedunculo subglabro quam petiolus breviore, spica florente quam limbus pluries breviore apice mucronulata, bracteae cucullatae glabrae vertice triangulari; antheris subglobosis filamenta aequantibus, stigmatibus linearibus.

Ramuli lenticellis parvis conspersi, collenchyma in fasciculos discretos dispositum zona interna sparsim libriforme. Limbi in sicco membranacei usque ad 19 cm. longi et 10 cm. lati. Petioli usque ad limbi latus longius 10 mm., inter limbi latera 2 mm., pedunculi 5 mm. longi. Spica florens 2.5 cm. longa, 1.5 mm. crassa. Stamina 4. Stigmata 3 sessilia.

COSTA RICA: Bois frais au pied des collines de Chirripó, alt. 100 m., *H. Pittier* 16061.

PIPER CITRIFOLIUM Lam., γ **Cookii,** n.var.—Ramulis glabris, limbo ovato-lanceolato basi inaequilatera altero latere rotundato altero acuto, usque ad 14.8 cm. longo et 5.9 cm. lato.

GUATEMALA: Near the Finca Sepacuité, Alta Verapaz, *O. F. Cook* and *R. F. Griggs* 697.

Piper subcitrifolium, n.sp.—*Piper uspantanense* C. DC. BOT. GAZ. **19**:6. 1894, in part.—Ramulis glabris; foliis brevissime petiolatis, limbo elliptico-lanceolato basi inaequilatera utrinque acuto, apice acute acuminato, supra glabro subtus ad nervos nerv ulosque minute velutino, nervo centrali nervos adscendentes utrinque 5 mittente quorum supremus fere a medio centralis solutus, petiolo puberulo basi ima vaginante; pedunculo subglabro quam petiolus breviore, spica quam limbus paullo breviore apice obtusa bracteae vertice truncato triangulari margine dense et flavide hirsuta,

pedicello aequilato margine hirtello, bacca inferne haud profunde in rhachi immersa et cum ea concreta, vertice pulposa et hirsuta.

Ramuli spiciferi 2.5 mm. crassi, collenchyma continuum zona interna sparsim libriforme, fasciculi intramedullares 1-seriati, canalis lysigenus nullus. Limbi in sicco membranacei creberrime et minute pellucido-punctulati, usque ad 13 cm. longi et 6 cm. lati. Petioli usque ad limbi latus longius fere 10 mm., inter limbi latera 2 mm., pedunculi 6 mm. longi. Spica matura 10 cm. longa usque ad 3.5 mm. crassa. Stamina 4; baccae flavicantes. Stigmata 3 sessilia.

GUATEMALA: Cerro Gordo, Depart. Santa Rosa, *J. D. Smith* 3827.

Piper triseriale, n.sp.—Ramulis hirtellis; foliis sat longe petiolatis, limbo ample ovato basi modice inaequilatera utrinque truncato-rotundato, apice brevissime acuminato, supra glabro subtus ad nervos nervulosque hirtello, nervo centrali nervos adscendentes utrinque 5 mittente quorum supremus fere e medio centralis solutus, nervis lateralibus utrinque 3 a basi solutis, petiolo subtus hirsuto usque ad limbi latus brevius vaginante stipulis dorso hirtellis; pedunculo glabro petiolum aequante, spica limbum aequante vel paullo superante, bracteae cucullatae vertice inflexo rotundato-triangulari pedicelloque calceoliformi margine hirsutis, antheris reniformibus parvis, bacca glabra submatura rotundato-subtetragona, stilo brevi, stigmatibus linearibus.

Ramuli spiciferi circiter 8 mm. crassi in sicco nigri, collenchyma in fasciculos discretos dispositum et haud libriforme, fasciculi intramedullares 3-seriati, canalis lysigenus nullus. Limbi in sicco coriacei pellucido-punctulati, usque ad 30 cm. longi et fere 20 cm. lati, in specimine verisimiliter abnormaliter inferne margine obtuse sinuato-dentati. Petioli usque ad limbi latus longius 6 cm., inter limbi latere 6 mm. longi. Spica fere matura 39 cm. longa, 6 mm. crassa. Stamina 4 basi baccae adnata. Stilus bacca multo brevior. Stigmata 3.

COSTA RICA: Forêts de La Palma, alt. 1459 m., *H. Pittier* 12663.

Piper dasypogon, n.sp.—Ramulis longe et fusce pilosis; foliis magnis modice petiolatis, limbo oblongo-elliptico basi valde inaequilatera profunde cordato, lobo majore auriformi petiolum velante, apice sat longe acuminato, supra laevi praesertim ad nervos subtus densius et ubique piloso, nervo centrali nervos adscendentes utrinque 3–4 mittente, quorum supremus fere a medio centralis solutus, nervis lateralibus 4 e basi in lobum majorem divaricantibus, petiolo subtus dense et longe piloso usque ad limbi lobum majorem

vaginante; pedunculo longe piloso gracili quam petiolus fere duplo longiore, spica quam limbus fere $\frac{1}{3}$ breviore, sat crassa, bracteae adultae glabrae inferne canaliculatae vertice cucullato subrotundo margine praesertim postice longe piloso, antheris rotundatis quam filamenta pluries brevioribus, ovario glabro in stilum attenuato, stigmatibus linearibus.

Ramuli spiciferi circiter 4 mm. crassi, collenchyma haud libriforme in fasciculos discretos dispositum, fasciculi intramedullares 1-seriati, canalis lysigenus unicus centralis. Limbi in sicco firmi opaci et pellucido-punctulati usque ad 32 cm. longi et 14 cm. lati. Petioli usque ad limbi latus longius 3.5 cm., inter limbi latera 7 mm. longi, lobus basilaris major fere 7 cm. longus. Pedunculi 7.5 cm. longi. Spicae usque ad 6 mm. crassae. Stamina 4 ad basin ovarii rhachi inserta, bacca verisimiliter stilifera.

COSTA RICA: Buenos Aires, alt. 2000 m., *H. Pittier* 10641.

Piper sinugaudens, n.sp.—Ramulis altero latere villosis; foliis brevissime petiolatis, limbo elliptico-oblongo basi inaequilatera cordulato, apice longe et acute acuminato, supra glabro subtus ad nervos nervulosque hirtello, nervo centrali nervos adscendentes utrinque 5 mittente quorum supremus a medio centralis solutus, petiolo dense hirsuto basi vaginante; pedunculo hirtello petiolum multo superante, spica quam limbus pluries breviore apice obtusiuscula, bracteae calceoliformis dorso hirsutae vertice triangulari margine hirsuto, antheris rotundatis filamenta fere aequantibus, ovario glabro apice in stilum attenuato, stigmatibus linearibus.

Ramuli spiciferi 2 mm. crassi, in 2.5 mm. crassis collenchyma in fasciculos discretos a latere valde productos dispositum et haud libriforme, fasciculi intramedullares 1-seriati, canalis lysigenus nullus. Limbi in sicco membranacei obscure virides parce pellucido-punctulati, superi usque ad 17.5 cm. longi et 5.2 cm. lati. Petioli usque ad limbi latus longius et inter limbi latera 2 mm., pedunculi 12 mm. longi. Spicae florentes 5.2 cm. longae, 2 mm. crassae. Stamina 4. Stigmata 2.

COSTA RICA: Buena Vista, road to San Carlos Valley, alt. 600 m., in deep ravine, *O. F. Cook* and *C. B. Doyle* 150.

Piper calcaratum, n.sp.—Ramulis glabris; foliis breviter petiolatis, limbo oblongo-obovato basi leviter inaequilatera altero latere subrotundato altero acuto, apice acute acuminato, supra glabro subtus ad nervos puberulo, nervo centrali nervos adscendentes utrinque 7 mittente quorum supremus fere a 13.5 cm. supra basin solutus, petiolo glabro usque ad limbum vaginante;

pedunculo glabro petiolum fere aequante, spica florente quam limbus fere triplo breviore apice mucronato, bractea lata florem antice amplectente glabra inferne dorso longe calcarata, calcare subulato, ovario stiloque glabris, stigmatibus brevibus linearibus.

Ramuli spiciferi circiter 4 mm. crassi, collenchyma in fasciculos discretos dispositum et zona interna sparsim libriforme. Limbi in sicco membranacei minute pellucido-punctulati, circiter 26 cm. longi et 12.5 cm. lati. Petioli usque ad limbi latus longius fere 20 mm., inter limbi latera fere 3 mm. longi. Spica florens circiter 7 cm. longa et inferne cum stilis circiter 7 mm. crassa, bracteae calcar 1 mm. longum. Stamina 4 ad imam basin baccae rhachi inserta, stilus 2 mm. longus. Stigmata 3.

COSTA RICA: Forêts de Las Vueltas, Tucurrique, alt. 635 m., *H. Pittier* 13185.

Piper acuminatissimum, n.sp.—Ramulis glabris; foliis modice petiolatis glabris, limbo oblongo-elliptico-lanceolato basi aequilatera acuto, apice sat longe et acute acuminato, nervo centrali nervos adscendentes utrinque circiter 10 mittente quorum supremus supra medium centralis solutus, petiolo basi ima vaginante; pedunculo glabro quam petiolus breviore, spica submatura quam limbus pluries breviore, bractea galeato-ovata glabra rhachi glabra, baccis sublaxe dispositis subtetragonis glabris, stigmatibus brevibus linearibus.

Ramuli spiciferi fere 2 mm. crassi, collenchyma in fasciculos discretos dispositum et omnino libriforme, fasciculi intramedullares 1-seriati, cellulae flavidae in medulla et in cortice sparsae. Limbi in sicco membranacei et virescentes, crebre pellucido-punctulati usque ad 17 cm. longi et 6.5 cm. lati. Petioli usque ad 18 mm., pedunculi 6 mm. longi. Spicae submaturae fere 4 cm. longae. Stamina 4. Baccae in sicco rubrae, fere 3 mm. longae. Stigmata 4 sessilia.

COSTA RICA: Plaines du San Carlos, alt. 100 m., *H. Pittier* 16321.

PIPER PULCHRUM C. DC. **γ copeyanum,** n.var.—Limbo basi fere aequilatera profunde cordato vel breviter peltato apice obtuse acuminato, usque ad 18 cm. longo et fere 11 cm. lato; spica submatura quam limbus paullo longiore.

COSTA RICA: Forêts de Santa Rosa de Copey, alt. 1800 m., *H. Pittier* 12198.

STUDIES IN EVAPORATION AND TRANSPIRATION[1]

GEO. F. FREEMAN

(WITH FIVE FIGURES)

As the result of studies extending over several years, considerable experimental data have been accumulated concerning the transpiration of alfalfa and other plants under various accurately measured conditions of temperature, relative humidity, and wind movement. It was found, however, that the interpretation of these results was hopeless unless something more was known about the quantitative influence of these factors upon purely physical evaporation than was available to the writer. Thus it was impossible to say whether a given result was simply the product of the physical factors then obtaining, or to what extent it was modified by the physiological reactions of the plant itself. One should be able to calculate from rational formulae the behavior of a physical evaporating surface for the given conditions. Any departure from this result could then be attributed to the response of the living organism.

It may be assumed that the general type of such a formula will remain the same for all situations, but that the constants will vary with all of the varying conditions of environment, temperature, wind movement, relative humidity, and size and nature of the evaporating surface. The purely physical experiments here reported were designed, first to work out the generalized type of the formula, and then to obtain the constants for certain special cases of environment and other factors. Environment is used here in a restricted sense, meaning only the size and nature of the space within which the evaporating surface is inclosed. In the work reported this was one liter of space included within a glass cylinder closed by two large rubber stoppers at either end. When

[1] These experiments were conducted at the University of Arizona Agricultural Experiment Station during the writer's connection with that institution, which extended over the years 1909–1918. They were, for the most part, conducted during the latter part of this period.

a surface is evaporating in the open, the environment is unbounded or indefinite. It differs from the closed environment, not in type, but in degree, since where there is any wind movement, after a greater or less length of time, the evaporating surface will come into equilibrium with it, and thereafter give off water at a uniform rate. The larger the environment and the slower the wind movement, the longer will be the time required to reach this equilibrium. With an unbounded environment and no wind movement, theoretically it would never be reached, but for all practical purposes a small evaporating surface exposed in the open in still air soon reaches a uniform rate of evaporation, which will remain constant so long as the temperature and dewpoint of the air remain the same. The influence of the size of the environment, therefore, is capable of mathematical expression, and may enter as a factor in a rational evaporation formula. When the size of the environment always remains the same, as in all the experiments conducted by the writer, this factor may be left out of the formulae as a variable, that is, its value may be included in one of the other constants found. When the size or nature of the environment varies in any way, it must be calculated as a separate constant, or else the other constants (which had included it) must be recalculated for each new environmental condition. It is this consideration which has made it impossible to write, for any given type of surface, an evaporation formula which would apply to all situations, even though all be in the open. The reason for this is that every environment is more or less restricted by buildings, trees, banks, hills, or mountains, so that no two are exactly alike. It would be impossible to write a formula which would account for all of these variations. So long, however, as we confine ourselves to a given environment and a given type of evaporating surface, we can easily account for variations in amount of surface, temperature, wind movement, and dewpoint of the air.

In the physical experiments undertaken, the evaporating surface used was a porous cup atmometer. A constant stream of air was drawn through the cylinder (over the atmometer) by a rotary air pump driven by a small motor. The air was measured by a water gasometer which was accurate to 1/1000 of a cubic foot.

The dewpoint of the incoming and outgoing air was determined by the interjection of the base of a polished nickel test-tube into the air stream. Ether within the tube was cooled by blowing a current of air into it with an atomizer bulb. When the ether and the tube were cooled to the dewpoint of the air stream, the formation of a film of dew on the outside of the test-tube could be observed. A delicate thermometer having its bulb immersed in the ether was then quickly read to 0.1 of a degree, which appeared to be sufficiently accurate for all practical purposes. In the following discussion only the dewpoints of the incoming and outgoing air are given. Anyone desiring to know the absolute evaporation can quickly calculate it from these data; but for the purposes of this discussion this is not necessary. Let y = rise in dewpoint of outgoing air over that of the incoming air; t = temperature of air; t_1 = dewpoint of incoming air; z = a constant, the value of which will depend upon the rate of air movement (w) and the size and nature of the evaporating surface. The value of y may then be expressed by the formula $y = z(t - t_1)$. The agreement of this formula with the experimental results is shown in fig. 1. This gives the results of an experiment in which the temperature was artificially raised and controlled, giving a range from 16.4 to 25.2° C. Since the dewpoint of the air used remained constant at 3.0°, there was a range in the value of $t - t_1$ of 8.8°. The lines ot and ot_1 give the value of t and t_1 respectively. The line oy gives the calculated value of y when $z = 53$ per cent. The dots show the agreement of the experimental with the calculated value of y. So long as other factors remain the same, the value of y appears to

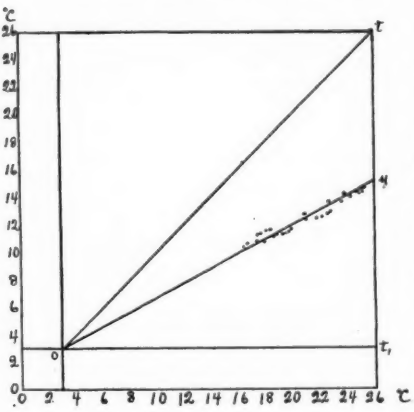

FIG. 1

be a constant linear proportion of the rise of t. A number of other experiments were made which exhibited a similar agreement between the experimental and calculated results. All of these

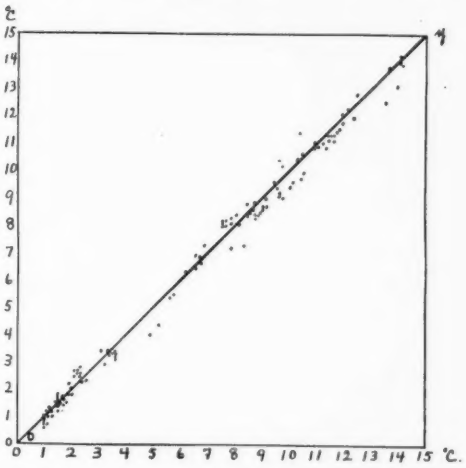

FIG. 2

are summarized in fig. 2, in which the ascending line oy represents the calculated value of y, while the dots show the experimental results obtained.

Effect of wind movement

It has been stated that the value of z depends upon the rate of air movement (w) and the extent and nature of the evaporating surface. When the latter remains unchanged and only wind movement is varied, z takes the form of $z=\frac{1}{1+c(w)^n}$, in which c and n are constants. The formula then becomes $y=\frac{t-t_1}{1+c(w)^n}$. In using this formula it is convenient to plot the results as is shown in fig. 3; ot is the temperature of the air, and o_1t_1 is its dewpoint; both of which are here constant at 21° and −1.8° respectively. The rate of wind movement may be plotted along o_1t_1, from which the found values of y may be plotted as ordinates. The curved line oy joining these ordinates then gives the value of y, which is

seen to decrease as the rate of wind movement is increased. Now let a line bisecting the right angle at o cut oy at c. The ordinate from o_1t_1 passing through c will give a value of w which may very conveniently be used as the unit. Now since $1^n = 1$, the value of y at this point becomes $y = \frac{t - t_1}{1 + c}$; hence $c = \frac{t - t_1}{y} - 1$. By substituting this value of c into the formula with other experimental values of y and w, the value of n can be obtained readily. A more general

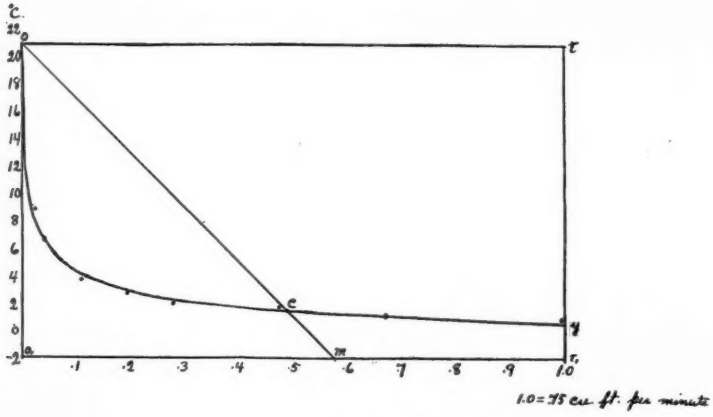

FIG. 3

method of finding the value of n is by the elimination of c, as follows: Going back to the original formula and solving for cw^n, we find that: $cw^n = \frac{t - t_1}{y} - 1 = p$; likewise $cw_1^n = \frac{t - t_1}{y_1} - 1 = p_1$; dividing $\left(\frac{w}{w_1}\right)^n = \frac{p}{p_1}$; whence $n = \frac{\log \frac{p}{p_1}}{\log \frac{w}{w_1}}$.

Knowing the value of n, we can readily find c by the formula $c = \frac{p}{(w)^n}$. The first method for finding the value of c and then of n is quicker and more accurate when as many as four or five experimental points on the curve oy are known, thus enabling one to

locate the point c with reasonable accuracy. When only two or three points are known, however, the second method should be used. By the first method, when 0.485 cu. ft. of air per minute was the unit of wind movement, the values of c and n were found to be 5.706 and 0.5 respectively. With these data the complete theoretical curve oy may be calculated and plotted, and the provisional curve used in finding the point c corrected and extended.

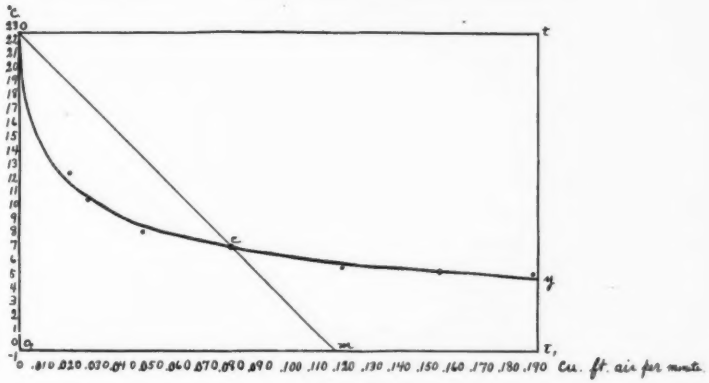

FIG. 4

In fig. 3 the complete curve given is the calculated theoretical curve, and the dots show the close adaptation of the experimental data to it. The agreement appears almost strikingly complete.

Fig. 4 gives an experiment of a similar nature in which $n = 0.58$ and $c = 2$. In this figure the wind movement is drawn on a larger scale than in fig. 3. As will be seen later, the factor c includes both the corrections for the area and the nature of the evaporating surface, and to adjust the temperature and wind movement factors to each other. The correspondence of the experimental results with the theoretical curve is again quite close, as is shown by the dots.

It now remains to determine the influence of changes in the area of the evaporating surface, assuming that its character remains constant. Changes in the evaporating area will affect both c and n. As the area at which c is determined rises, the value

of c is diminished; and when the evaporating surface practically fills its environment, c approaches zero. On the other hand, as the area at which c is determined is made smaller, the value of c indefinitely increases.

As the evaporating area increases, the value of n increases, until when the evaporating area practically fills its environment, the value of $n=1$ (that is, the air passing off will be saturated and the evaporation will be in direct linear proportion to the rate of wind movement). Conversely, when the size of evaporating area is diminished, the value of n decreases, until it reaches the vanishing point, when the evaporating area becomes indefinitely small. When n becomes zero, the value of w^n will equal 1, regardless of the numerical value of w, since any number raised to the zero power equals one. In other words, when the evaporating area is indefinitely small, it cannot measurably increase the humidity of the surrounding air; hence changes in wind movement would have no effect upon the rate of evaporation. Instead of c we may therefore write $\frac{c}{a}$, and for n write $\frac{a}{k+a}$, in which a is any area expressed in terms of the area used when c was determined, and k is a constant. The formula then becomes $y=\frac{t-t_1}{1+\frac{c(w)^{\frac{a}{k+a}}}{a}}$. Again, if the wind movement used when c and k were determined be made unity, and other wind movements be expressed in terms of it, since 1 raised to any power is 1, the formula for that wind movement becomes $y=\frac{t-t_1}{1+\frac{c}{a}}$, from which the value of c can readily be calculated from any experimental value of y. This statement of the formula can also be used in experiments in which the wind movement is not varied, and may hence be considered as unity. The details of such an experiment are given in table I, where $c=0.984$, $w=1$, $a=1$, and $a_1=1.654$. Since $w=1$ throughout, the determination of k was unnecessary.

Table II gives another experiment of a similar nature, in which the wind movement was 91.43 liters of air per hour throughout, which

TABLE I

EVAPORATION EXPERIMENT WITH ATMOMETER

Temperature outside	Dewpoint outside	Dewpoint of escaping air	Evaporating surface	Found y	Calculated y	Difference
27.0.....	0	13.8	45.8 sq. cm. = 1	13.8	13.5	−0.3
26.0.....	0	13.2	45.8 sq. cm. = 1	13.2	13.0	−0.2
26.0.....	0	12.8	45.8 sq. cm. = 1	12.8	13.0	+0.2
25.9.....	0	12.8	45.8 sq. cm. = 1	12.8	13.0	+0.2
	Average		.....	13.2	13.1	−0.1
27.0.....	0	16.2	75.47 sq. cm. = 1.645	16.2	16.8	+0.6
26.0.....	0	16.2	75.47 sq. cm. = 1.645	16.2	16.2	0
26.1.....	0	15.8	75.47 sq. cm. = 1.645	15.8	16.2	+0.4
26.1.....	0	16.0	75.47 sq. cm. = 1.645	16.0	16.2	+0.2
	Average		.....	16.1	16.4	+0.3

is here used as unity. The other constants were as follows: $c = 1.257$, $a = 42.04$ sq. cm., here taken as unity, and $a_1 = 75.47$ sq. cm. $= 1.7954$.

There remains to show the details of an experiment in which both the area and wind movement were varied. Here $a = 52.98$

TABLE II

EVAPORATION EXPERIMENT WITH ATMOMETER

Temperature outside	Dewpoint outside	Dewpoint of escaping air	Evaporating surface	Found y	Calculated y	Difference
21.7.....	1.0	10.6	1	9.6	9.2	.....
21.5.....	1.0	10.2	1	9.2	9.1	.....
21.2.....	1.0	10.0	1	9.0	8.9	.....
21.0.....	1.0	10.4	1	9.4	8.9	.....
20.9.....	1.1	10.0	1	8.9	8.8	.....
20.8.....	1.1	10.1	1	9.0	8.7	.....
20.8.....	1.2	10.2	1	9.0	8.7	.....
20.7.....	2.2	11.2	1	9.0	8.2	.....
20.7.....	2.3	10.5	1	8.2	8.1	.....
20.7.....	2.2	9.8	1	7.6	7.6	.....
	Average		.....	8.9	8.6	−0.3
21.7.....	2.2	13.6	1.7954	11.4	11.5	.....
21.6.....	2.3	13.5	1.7954	11.2	11.4	.....
21.4.....	2.3	13.6	1.7954	11.3	11.2	.....
21.0.....	2.2	12.7	1.7954	10.5	11.0	.....
21.0.....	2.2	12.8	1.7954	10.6	11.1	.....
	Average		.....	11.0	11.2	+0.2

sq. cm., taken as the unit of area, $a_1 = 75.47$ sq. cm. $= 1.42$, $k = 3.546$, $c = 1.076$; $w = 91.43$ liters per hour, here used as unity, and $w_1 = 165.62$ liters per hour $= 1.816$.

The calculated and experimental results again agree so closely that the conclusion seems justified that they are within the limits of experimental error.

TABLE III

EVAPORATION EXPERIMENT WITH ATMOMETER

Temperature outside	Dewpoint outside	Dewpoint of escaping air	Evaporating surface	Wind movement	Found y	Calculated y	Difference
25.2.....	2.2	13.0	1	1.816	10.8	10.3	.....
25.1.....	2.2	12.7	1	1.816	10.5	10.3	.....
25.0.....	2.2	12.4	1	1.816	10.2	10.2	.....
24.9.....	2.2	12.3	1	1.816	10.1	10.2	.....
	Average		.....	.....	10.4	10.3	−0.1
25.3.....	1.0	13.0	1	1	12.0	11.7	.....
25.4.....	1.0	12.9	1	1	11.9	11.8	.....
25.4.....	0.9	12.7	1	1	11.8	11.8	.....
25.4.....	1.1	12.6	1	1	11.5	11.7	.....
25.4.....	1.0	12.4	1	1	11.4	11.7	.....
	Average		.....	.....	11.7	11.7	0.0
27.0.....	1.1	15.2	1.42	1	14.1	14.7	.....
26.8.....	1.2	15.2	1.42	1	14.0	14.6	.....
26.6.....	1.2	14.8	1.42	1	13.6	14.5	.....
26.4.....	1.1	16.0	1.42	1	14.9	14.4	.....
26.2.....	1.0	15.2	1.42	1	14.2	14.3	.....
26.1.....	1.0	15.3	1.42	1	14.3	14.3	.....
	Average		.....	.....	14.2	14.4	+0.2
26.0.....	1.2	14.2	1.42	1.816	13.1	13.1	.....
25.8.....	1.3	14.4	1.42	1.816	13.1	12.9	.....
25.4.....	1.4	13.6	1.42	1.816	12.2	12.6	.....
25.3.....	1.4	13.8	1.42	1.816	12.4	12.6	.....
	Average		.....	.....	12.7	12.8	+0.1

An examination in detail of the completed formula will show whether it will continue to appear rational when the several variables concerned are carried to their extreme limits. As t increases, y will increase indefinitely. As t decreases, y will decrease and vanish when t falls to t_1, or to absolute zero. As t_1 increases, y decreases and vanishes when t_1 reaches t. As t_1 decreases, y increases until t_1 reaches absolute zero, at which the size of y will depend on t, a, and w only. As a increases, the value

of the expression $\frac{c(w)^{\frac{a}{k+a}}}{a}$ decreases, until when a is indefinitely large it vanishes; hence the value of y will equal $t-t_1$, that is, the air will be saturated for the temperature t. At the same time the expression $\frac{a}{k+a}$ will approach 1; that is, as the size of the evaporating area increases in relation to its environment, the more dependent is the rate of evaporation upon the wind movement. On the other hand, if a decreases, the value of the expression $\frac{c(w)^{\frac{a}{k+a}}}{a}$ increases and approaches infinity, at which point y would equal zero. At the same time the expression $\frac{a}{k+a}$ will approach zero. In other words, when the evaporating area decreases, the rate of evaporation depends less and less upon the wind movement. As w increases, the value of y will decrease, and vanish when w reaches infinity. As w decreases, y will increase; and when w becomes zero, the value of y will equal $t-t_1$, that is, the air will become saturated for temperature t. It thus appears that the formula remains rational when any of its variables are projected to their extreme limits. Moreover, it appears to correspond, within allowable limits of experimental error, with the results obtained throughout the range of conditions covered by the work of the writer. This range does not include temperatures either above the boiling point or below the freezing point of water. Disturbing factors which might be introduced at those critical stages in the physical condition of water were not investigated, inasmuch as they would practically never be reached in investigations concerned with the transpiration of living plants.

Fig. 5 gives the results of an experiment made upon a potted alfalfa plant. The temperature was raised artificially by means of an electric current passed through a coil of nicrome wire. This was wrapped around the cylinder into which the branches were inserted from below through openings in the stopper. The opening through the stopper was sealed around the stems with low melting point paraffin. The temperature was controlled by regulating the current passing through the resistance wire by means

of a thermostat. Throughout this experiment the air stream was constant at 70.32 liters per hour, and the dewpoint of the exterior air was 4.8° C. The range of temperature was 17.8–36.1°. The range in the value of $t-t_1$ was 18.3°. The lines ot and ot_1 give the values of t and t_1 respectively. The line oy gives the calculated value of y where z [formula $y=z\ (t-t_1)$] equals 7.45 per cent. The dots show the agreement of the experimental with the calculated value of y.

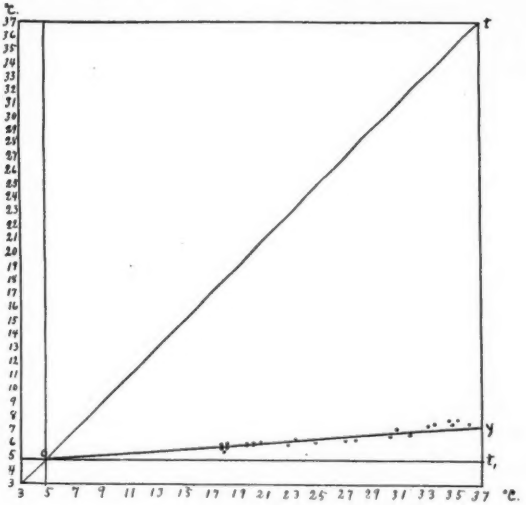

FIG. 5

This figure seems to indicate that under temperature changes of the magnitude here given, the plant acts essentially as a physical evaporating surface. On the other hand, when the relative humidity of the external air is varied, there appears to be a very decided response on the part of the plant, as is shown in the following experiment.

On March 14, 1914, a potted alfalfa plant was taken from the highly humid atmosphere of the greenhouse and brought to the much drier atmosphere of the laboratory, where the light also was not so intense as in the greenhouse. The stems of this plant were sealed into the evaporation cylinder as described (of course

TABLE IV

Time	Temperature		Liters air per hour	Relative humidity		Dewpoint found (x)		Dewpoint calculated inside (y)	Found divided by calculated
	Outside	Inside		Outside	Inside	Outside	Inside		
1:44	18.0	18.3	95	25	79	−3.5	14.4	13.9	1.04
1:47	18.0	18.1	95	25	77	−3.0	13.8	13.9	0.99
1:56 *a*	18.0	17.8	95	25	76	−3.0	13.3	13.3	1.00
2:02	18.0	17.6	95	25	73	−3.0	12.4	13.5	0.92
2:10				?	68	?	10.8	.....	.....
2:19 *b*	18.1	17.2	95	?	54	?	6.1	.....	.....
2:36 *c*	18.2	16.0	190	?	66	?	9.9	.....	.....
2:53 *d*	18.2	16.6	95						
	2:55 normal air								
3:02 *e*	18.2	16.8	95	24	71	−3.4	11.2	16.1	0.70
3:14 *f*	18.2	16.6	190	24	64	−3.4	9.4	13.5	0.70
	3:16 moist air								
3:36	18.2	18.0	95	79	91	14.3	16.4	17.3	0.95
3:44 *g*	18.2	18.2	95	81	93	14.7	17.0	17.5	0.97
3:54 *h*	18.3	18.2	190	82	94.2	15.1	17.2	17.2	1.00
3:58	18.4	18.2	95	82	96	15.1	17.5	17.3	1.01
4:04 *i*	18.4	18.3	95	82	97	15.1	17.8	17.7	1.01
	4:05 normal air								
4:09	18.4	18.1	95	28	95	−1.3	17.2	14.2	1.21
4:12	18.4	17.9	95	26	91	−2.3	16.3	13.9	1.17
4:16	18.4	17.8	95	26	85	−2.3	15.1	13.8	1.09
4:19 *j*	18.4	17.7	95	26	85	−2.2	15.0	13.7	1.10
4:24	18.5	17.6	95	26	83	−2.7	14.5	13.5	1.07
4:26	18.6	17.5	95	25	83	−2.6	14.4	13.5	1.07
4:29	18.6	17.4	95	25	81	−2.6	13.9	13.4	1.04

without removing them from their own roots growing in the pot), a current of air was drawn over them, and successive readings made, as shown in table IV.

Since the area of leaves was not changed in table IV, the simpler form of the formula $y=\frac{t-t_1}{1+c(w)^n}$ could be used; c was taken as 0.25 and n as 0.93. This high value of n is in keeping with the fact already mentioned, that when the evaporating area is large in comparison with its environment, the value of n will be large. Sixty-two leaves, having an area of approximately 200 sq. cm., were on the stems included within the cylinder. Thus it may be noted that the value of y for the slower wind movement averaged 80 per cent of the value of $t-t_1$. In this experiment both the wind movement and the humidity of the air passed over the plant were varied. The latter was accomplished by (1) using the normal air of the room, (2) first passing the air through tubes of phosphorous pentoxide and then over the plant, and (3) passing over the plant a controlled mixture of saturated and normal air. It is not assumed that the air passed over the phosphorous pentoxide was absolutely dry, but its dewpoint was so low that it could not be detected by the ether-cooled mirror, which could be easily read down to -6 or $-7°$ C.

For the purpose of discussion the experiment may be divided into eight periods, as follows:

(*a*) 1:44–2:07, normal air, slow wind
(*b*) 2:07–2:32, dry air, slow wind
(*c*) 2:32–2:43, dry air, fast wind
(*d*) 2:43–2:53, dry air, slow wind
(*e*) 2:53–2:59, normal air, slow wind
(*f*) 2:59–3:16, normal air, fast wind
(*g*) 3:16–3:45, moist air, slow wind
(*h*) 3:45–3:55, moist air, fast wind
(*i*) 3:55–4:05, moist air, slow wind
(*j*) 4:05–4:29, normal air, slow wind

First compare the column showing the outside temperature with that exhibiting the temperature within the cylinder and measured by a thermometer having its bulb among the leaves. The temperature within the cylinder began 0.3° C. above that

outside, but slowly fell throughout periods *a*, *b*, and *c*, reaching its lowest point in the later period of dry air and high wind movement when it was 2.2° below that of the outside air. When in period *d* slow wind movement was used, the cylinder temperature rose 0.6°. In period *e*, when normal air was used, the cylinder temperature rose 0.2°. In *f*, when fast wind was again used, the temperature dropped 0.2°. When high humidity air was used in periods *g*, *h*, and *i*, and the transpiration was very low, the temperature rose to within 0.1° of that of the external air, but during period *j*, when normal air was used and the evaporation increased, the cylinder temperature steadily fell, until at the end of the experiment it was 1.2° below that of the exterior air. We thus have a definitely measurable cooling effect of evaporating leaves upon the air which passes over them.

In order to study the physiological response of the plant foliage as an evaporating surface, the column giving the dewpoint inside (the dewpoint of the air after it has passed over the plant) may be compared with the next column, which shows the calculated values, considering the leaves as physical evaporating surfaces and using the constants already given. To facilitate this comparison the last column is added to give the ratio of the found to the calculated dewpoint.

It is estimated that the time required to bring the plant from the greenhouse and instal it in the transpiration apparatus and obtain the first reading was about half an hour. Suppose the evaporating condition at this time to be 104 (see last column of table). By the end of period *a*, with the plant exposed to the drier laboratory air (23 minutes), this had dropped to 92. During periods *b*, *c*, and *d* (46 minutes) the plant was exposed to air which had passed over phosphorous pentoxide. Although the comparison of the calculated with the found results cannot be made here, it may be observed that the dewpoint during period *d* was lower than during period *b*, which indicates a still further restriction of evaporation. When the plant was put back on normal air in period *e*, it was found that this restricting influence had cut down the found dewpoint to 70 per cent of the calculated value, and that this was maintained throughout the 23 minutes of periods *e*

and *f*. When, however, a stream of very moist air (relative humidity 79–82 per cent) was used, the plant again responded, and within 20 minutes (reading at 3:36 P.M.) had reached an evaporation rate of 95 per cent of the calculated value. This increase continued until at 4:04 (28 minutes later) it was 101. When the shift was again made to normal air (at 4:05) there was exhibited at 4:09 (4 minutes later) a special emphasis of this high transpiring condition of the plant, since it gave a reading of 121 per cent of the calculated value. The effect of the drier normal air soon became apparent in the steady fall of this ratio, which at 4:29, or 24 minutes after removal of the moist air, had reached a value of 104, which was identical with its value at the beginning of the experiment, when it had likewise been removed from the saturated air of the greenhouse some 25 or 30 minutes previously.

The response of the plant to the humidity of the air is strongly indicated here. This response is rapid but not immediate. In looking over a number of experiments similar to the one described, it appears that when the humidity is suddenly changed but remains constant thereafter, complete adjustment is usually attained in 30–35 minutes.

It may be recalled that in the experiment involving changes in temperature only (fig. 5), the plant leaf acted approximately as a physical evaporating surface. This was true in spite of the fact that the change in the temperature of the air passing over the plant also involved a considerable change in its relative humidity. Its actual dewpoint, that is, the water contained per liter, remained constant. At the higher temperatures the actual dewpoint of the air after passing over the plant was always higher than at the lower temperatures; that is, the leaves were evaporating more into an air of higher dewpoint than at the lower temperatures. This fact approximately offsets the effect of the greater water demand made upon the plant by the greater transpiration at the higher temperature, and gives a result which is very close to the behavior of a physical surface. When, however, the water content, that is, the dewpoint of the incoming air, is increased (other conditions remaining the same), the evaporation, or the water demand upon the plant, is strongly reduced.

We may infer from this that the guard cells of the stomata become more turgid, making these openings larger, and thus increase the evaporation coefficient of the surfaces.

The use of this formula in interpreting the results of comparative tests of the transpiration of different varieties or species of plants may be illustrated by two examples. The first may be taken from seven experiments made upon a peach tree (*Prunus persica*) and a large greasewood shrub (*Covillea mexicana*), which were growing in close proximity upon well cultivated and watered soil on the grounds of the University of Arizona. The data of this experiment are given in table V, which includes the temperature within the cylinder, the dewpoint of the external air, the dewpoint of the air coming out of the cylinders, the relative humidity of the same, and the number of square centimeters of leaves used. There is then placed in the last column a calculated "standard dewpoint," which is found by means of the formula, and is the dewpoint of the outgoing air which would have been given by a physical surface of the same evaporating potentiality as the given leaves (at the time when the experiment was made), but having an area of 100 sq. cm., a cylinder (air) temperature of 30° C., and an external dewpoint of 10° C. The wind movement in all cases was the same, being approximately 85 liters per hour. It will be noted in column *e* that the dewpoint of the escaping air from the greasewood cylinder was higher three times and lower four times than the dewpoint of the air escaping from the peach cylinder. When, however, each is calculated to the standard dewpoint, that of the air from the greasewood cylinder was always higher. It is surprising to find that the leaves of the greasewood (a strictly xerophytic plant) show such a uniformly higher transpiration rate than those of the peach (a deciduous mesophyte). It is interesting to note, therefore, that, whereas 100 sq. cm. of the greasewood leaves weighed 3.93 gm., a similar surface of peach leaves weighed only 1.92 gm. When the calculations were based upon equal weights of herbage, the peach showed an equally uniform greater transpiration per 100 gm. green weight foliage. The greasewood experimented upon was growing in the orchard where it received an abundance of irrigating water. Its leaves

TABLE V

Date (a)	Plant (b)	Temperature in cylinder (c)	Dewpoint of external air (d)	Dewpoint of escaping air (e)	Relative humidity of escaping air (percentage) (f)	No. of sq. cm. of leaves used (g)	Standard dewpoint (h)	Excess of greasewood
May 21	Greasewood	31	−4.3	21.9+	60	149.7	23.2	+4.3
	Peach	30	−4.3	18.5	53	249.4	18.9	
May 22	Greasewood	33	+0.9	24.2+	61	122.2	23.7	+1.3
	Peach	29	+0.9	22.7	70	211.5	22.4	
May 22	Greasewood	35	−2.7	23.5−	54	100.3	23.9	+1.9
	Peach	33	−2.7	24.3	62	206.5	22.0	
May 23	Greasewood	34	−1.7	29.8−	81	178.8	26.1	+0.1
	Peach	34	−1.7	30.1	82	204.8	26.0	
July 1	Greasewood	38	−6.7	28.4+	60	106.5	25.5	+6.2
	Peach	38	−6.7	19.4	36	160.9	19.3	
July 5	Greasewood	39	+6.1	26.7−	52	94.8	22.8	+5.7
	Peach	42	+6.1	28.2	50	203.1	17.1	
July 12	Greasewood	36	+9.5	26.9−	58	64.9	24.9	+4.6
	Peach	37	+9.5	27.0	59	116.1	20.3	

were very thick, green, and luxuriant, being markedly different from those growing on the dry mesa a few hundred yards distant. A single experiment comparing the orchard greasewood with that of the mesa gave a standard dewpoint 2° higher for the former. This indicates that its leaves had undergone a modification which favored a greater transpiration rate.

As an example of the use of this method in the study of the comparative water loss from different varieties of a single species, a set of eight experiments extending over a period of about two weeks may be given. These were upon two pure lines of alfalfa nos. 91 and 17. The results are collected in table VI, which has the same arrangment of material as table V. The dewpoint of the escaping air was greater for the cylinder covering branches of race no. 91 three times and less four times, but when calculated to the same standard dewpoint as used in table V, it was greater from race no. 91 for six out of the seven experiments made. These results, which would appear hopelessly confusing at first, when calculated to the standard dewpoint, seem to indicate with a fair degree of definiteness that the leaves of race no. 91 offered less hindrance to evaporation than did those of race no. 17. Here again it was the thicker leaves which gave the greater transpiration rate, since the average weight per 100 sq. cm. of race no. 91 was 2.57 gm., whereas that of race no. 17 was only 2.29 gm.

In comparing tables V and VI it will be noted that the differences in the standard dewpoints of the same species or variety for different days was often as great as or greater than the differences between the species or varieties being compared on the same day. In spite of this, however, the differences between the species or varieties were so constant that one cannot but believe they were real and significant. The differences in the standard dewpoints for different days must be sought therefore in some common factor which has influenced both types alike.

Such a factor, as shown in table IV, is the dewpoint of the external air. In examining tables V and VI it will be noted that whereas high standard dewpoints are perhaps more frequently than otherwise accompanied by high external dewpoints, this is

TABLE VI

COMPARISON OF TRANSPIRATION OF TWO PURE RACES OF ALFALFA

Date	Race no.	Temperature in cylinder	Dewpoint of external air	Dewpoint of escaping air	Relative humidity of escaping air	No. of sq. cm. of leaves	Standard dewpoint	Excess of race no. 91
May 12...	91.....	31	−0.2	19.4+	52	91.7	23.0	+1.6
	17.....	31	−0.2	16.2	43	82.8	21.4	
May 13...	91.....	27	0.0	17.2+	57	97.2	22.9	+2.1
	17.....	28	0.0	15.3	48	101.9	20.8	
May 14...	91.....	22	+3.0	15.7−	69	77.7	24.4	+0.5
	17.....	23	+3.0	15.9	66	79.6	23.9	
May 14...	91.....	25	−1.1	16.9−	66	79.4	24.5	−0.7
	17.....	24	−1.1	17.4	64	87.9	25.2	
May 15...	91.....	26	−1.0	17.4+	58	71.4	25.0	+0.2
	17.....	22	−1.0	16.0	70	99.5	24.8	
May 19...	91.....	28	−1.3	19.6−	61	83.3	25.0	+0.6
	17.....	26	−1.3	20.6	71	156.3	24.4	
May 20...	91.....	30	+2.4	23.9−	72	75.5	26.5	+0.5
	17.....	30	+2.4	24.6	75	103.4	26.0	

by no means always the case. There are other factors, for instance, such as the amount of light reaching the plant on more or less cloudy days, the age of the plants, and moisture content of the soil, all of which certainly affect the condition of the stomata and hence the evaporating efficiency of the leaves. These would, moreover, affect both types approximately alike.

Another disturbing factor, which would not equally affect the plants, is the area of foliage of each inclosed in the evaporating chamber. If such an amount of foliage is inclosed in one cylinder as to give its outgoing air a markedly higher dewpoint than that of the other cylinder, the evaporating rate per unit surface will be cut down by the greater relative humidity in the cylinder. The water demand upon a given area of the leaves will be reduced, and they will respond by opening wider their stomata. This will give the leaves of this cylinder a greater standard dewpoint than will be found for the leaves in the cylinder having the less surface exposed. In practical work, therefore, it is necessary either to inclose in each cylinder an approximately equal area of leaves (which is extremely difficult), or to so vary the wind movement as to have the dewpoint of the air, coming off each cylinder, approximately equal. This can be easily accomplished in the apparatus used by the writer, by pinching down the air supply tube of one or the other cylinders with a screw clamp.

Summary

1. As a result of evaporation experiments carried out by means of a porous cup atmometer inclosed in a glass cylinder of one liter capacity, through which an air current is passed, an evaporation formula is offered which may take any of the following forms:

$$\text{(a) } y=z(t-t_1);\ \text{(b) } y=\frac{t-t_1}{1+c(w)^n};\ \text{(c) } y=\frac{t-t_1}{1+\frac{c(w)^{\frac{a}{k+a}}}{a}}.$$

In these formulae y = rise in the dewpoint of the air caused by the loss of water to it of a given evaporating surface; t = temperature of the air; t_1 = dewpoint of the outside air; z = constant used when the area and wind movement remain constant; n = exponent of w, used when the area remains constant; c = constant coefficient

of w, used either when the area is constant (when a does not appear in the formula) or when a varies and hence appears in the formula; a = area of the evaporating surface which is always expressed as the ratio of the surface exposed to that exposed when c and k were determined; when c and k are determined, the area then used is taken as unity and all other areas expressed in terms of it; k = constant used in the exponent of w to adjust the area unit to the wind movement unit.

2. These formulae appear to be general in type and capable of use in any situation where y is measurable. It is possible that with some modification these formulae may also be of use when y cannot be measured, but where it is possible to measure directly the actual evaporation per unit area.

3. Under temperature changes only, alfalfa leaves appear to act as physical evaporating surfaces.

4. Changes in the dewpoint of the air result in profound changes in evaporating efficiency of leaf surfaces. This is probably a result of the opening and closing of the stomata.

5. It is possible to make use of these formulae in comparing the evaporating efficiency of different species of plants and interpreting results which would otherwise appear hopelessly confusing.

6. Distinct pure races of alfalfa exhibit measurable differences in the rate of evaporation per unit area of their leaves. Such differences may be of economic value in semi-arid or irrigated regions where production depends principally upon the efficiency of the use of the available water supply.

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EARLY DEVELOPMENT OF INOCYBE

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(WITH PLATES XVIII–XXII)

During a collecting trip with Professor ATKINSON at Coy Glen, near Ithaca, New York, on August 25, 1914, we came upon a large quantity of *Inocybe infelix* in all stages of development. At that time Professor ATKINSON was particularly interested in obtaining *Inocybe* material, as he had in mind the publication of a monograph of the genus. He felt that, before the systematic relationship could be determined with absolute certainty, there was need for more morphological work on the developmental stages of these plants. Accordingly he turned over this material to me as a nucleus of a paper on the development of *Inocybe*. Two years later, in July, while collecting fungi in the Adirondacks near Seventh Lake, material of *I. eutheloides* and *I. geophylla* was added, the latter collected by Miss LENA B. WALKER. In the following summer the same locality furnished *I. hystrix*, collected by Professor ATKINSON. The *I. obscura* material came from a hard gravelly path in Coy Glen on September 24, 1916.

All the *Inocybe* forms studied here are ground-inhabiting, and were collected from places where the soil was compact and comparatively poor in humus. The determinations were made by Professor ATKINSON from mature plants springing up from the same mycelium as the young buttons taken for study.[1] It is certainly to be regretted that this paper was not put forward at that time, before the untimely death of Professor ATKINSON, who felt so keenly the need of a closer cooperation of the systematist with the morphologist in working out plant relationships. The

[1] Plants were fixed in the field in medium chromo-acetic acid, care being taken to remove as much of the soil as possible before dropping them into the fluid. The washing afterward removed most of the gritty particles. After dehydration they were cleared in cedar oil and imbedded in 52° paraffine. Sections were cut 5–7 μ in thickness and stained with fuchsin, after having been previously treated with tannic acid. This method had been found to be most satisfactory for photographing other forms of agarics (**9**), and proved equally efficient in this case.

development proved to be so similar in all the forms studied that it will be unnecessary to describe it separately for each one. Accordingly, a general account of the method of growth will be given and any minor specific variations noted from time to time.

PRIMORDIUM OF BASIDIOCARP.—Very young stages in the development of the fruit body were found in only two of the five species, in *I. hystrix* (fig. 53) and *I. geophylla* (fig. 70). The button of *I. hystrix* measures 0.6×0.35 mm., and is composed of loosely interwoven hyphae ranging from 2 to 3 μ in diameter. In the basal end there is a more deeply staining region, conical in shape, where the elements are considerably thicker. This represents the primordium of the stem whose hyphae, multiplying very rapidly, are advancing into the fundamental tissue above. The young button at the right in fig. 70 of *I. geophylla* is composed of interlaced fibers 1–2 μ thick in the denser stem primordial region inside and 2–4 μ on the outside, where apparently they are disintegrating and wearing off through the contact with the soil.

DIFFERENTIATION OF PILEUS AND STEM PRIMORDIA.—The dome-shaped stem primordium at the base of the fruit body continues to advance upward within the fundamental tissue. After a time the hyphae in the apical region, which have been branching profusely and twining in and out through the interstices of the young button, change their general upward direction and radiate outward on all sides (fig. 55). Thus the pileus fundament appears in the form of a more or less globular cap, separated by an annular furrow from the primordium of the stem below (figs. 1, 2, 21, 39, 54, 55, 71). This method of progressive differentiation of first the stem and then the pileus from the apex of the former has previously been described by MÖLLER (**10**) for *Rozites gongylophara*, by ATKINSON (**8**) for *Lepiota cristata* and *L. seminuda*, by DOUGLAS (**9**) and SAWYER (**12**) for species of *Cortinarius*, by SAWYER (**11**) for *Pholiota squarrosa*, *P. flammans*, and *P. adiposa*, and by WALKER (**13**) for *Tubaria furfuracea* among the endogenous forms.

BLEMATOGEN.—The remnant of the original fundamental tissue, still enveloping the fundaments of pileus and stem, becomes the true "universal veil," or, as we shall call it, the blematogen. This name was proposed by ATKINSON (**2, 3**) because of the indefi-

niteness in the application of the former term by the earlier writers. Although there are minor differences in its character and considerable variation in its final disposition, it has been found to be a homologous structure in all endogenous forms. In the *Amanita* type, as illustrated by *Amanitopsis vaginata* (4), the blematogen is separated from the pileus by a clean-cut cleavage layer and forms the volva. In all the other forms it becomes more or less "concrete" with the pileus, so that in the majority of cases it is impossible to distinguish where the pileus leaves off and the blematogen begins. In *Agaricus* forms (1, 2, 6) considerable blematogen enters into the formation of the cortex of the pileus. In others it becomes the cuticle (*Cortinarius anfractus* and *C. armillatus*, 9). Often it is shed in the form of scales (*Cortinarius distans*, 9) which may be mealy or powdery (*Lepiota cristata*, 8, *Coprinus micaceus*, 7). In *Pholiota* (11) scales are formed from the blematogen which partly gelatinize. Frequently fibrillose scales of blematogen persist in the mature plants, as in *Lepiota clepeolaria* (5) and *Coprinus comatus* (7).

In four of these species of *Inocybe* the blematogen is a very delicate structure, which very soon disappears from the surface of the pileus. In *I. obscura* (pl. XVIII), *I. infelix* (pl. XIX), *I. entheloides* (pl. XX), and *I. hystrix* (pl. XXI) the pileus seems to expand through the blematogen to the surface, where it gives off the characteristic silky *Inocybe* fibrils. There is a gradual transition in the size of the hyphae from the inner ones, about 2 μ in diameter in the denser region, to the loose radiating ones on the outside which measure 4–6 μ in thickness. These on the outside take the stain more deeply than those within, and behave generally as disintegrating hyphae.

The condition is slightly different in *I. geophylla*, which belongs to a section of the genus characterized by a pileus which does not crack and which is covered with interwoven fibrils. That these interwoven fibrils are of blematogenous origin seems clear from the fact that they appear in the early stages before the pileus primordium has advanced to the surface of the fruit body (fig. 71). They form a deeply staining thin envelope over the whole of the developing basidiocarp. This envelope might possibly be

considered as a "primary universal veil" or protoblem,[2] such as occurs in addition to the blematogen over the surface of young buttons of *Agaricus campestris*. It does not, however, show as a definite layer in buttons younger than the one shown in fig. 71, although there are hyphae more deeply stained and with larger diameters at the surface in some (fig. 70). The irregularity of the latter would seem to indicate that they are the ends of hyphae undergoing disintegration on account of their contact with the soil. No trace of a protoblem was found in the four other species. This of course may be due to the fact that it was washed off during the rather vigorous treatment necessary to remove the grit particles, but it hardly seems possible that no trace would be left had it existed. The envelope of interwoven fibrils persists in *I. geophylla* (pl. XXII) in the oldest stages collected, and forms here the outer portion of a duplex universal veil such as was described in *Cortinarius anfractus* and *C. armillatus* (**9**). From this loose fibrils arise (fig. 79). Within is a looser, much more delicate tissue with large air spaces. The latter becomes more or less concrete with the pileus at the apex of the fruit body, and shows most clearly between the pileus margin and the stem below the gill cavity.

PRIMORDIUM OF HYMENOPHORE.—Following the differentiation of the stem and pileus primordia, or possibly proceeding at the same time in *I. infelix* (fig. 21), the fundament of the hymenophore makes its appearance (figs. 3, 4, 16, 19, 22, 23, 35, 36, 40, 41, 47, 48, 72, 73). The hyphae in the annular furrow left between the pileus and stem multiply very profusely and turn perpendicularly downward from the more laterally directed fibers of the pileus trama. They become very rich in protoplasm, as shown by their propensity for stain. They are very slender, with more or less pointed ends, so that they are able to push their way easily through the ground tissue. Such a rapid increase in growth here, while practically none is taking place in the blematogen, brings about a stretching and finally a rupturing of the latter tissue, bringing about the formation of the annular cavity (figs. 3, 4). Usually a well defined annular cavity does not make its appearance until the fruit body is slightly older and the palisade layer is organized

[2] See ATKINSON (**2, 3**) for a definition of this term.

(figs. 24, 25, 37, 42, 56, 74). At first the extent of growth of these fibers is very unequal, and in consequence the primordial surface is very uneven. Gradually, however, the ends of the hyphae become more blunt and even, and beginning at the stem a palisade layer commences to extend outward toward the margin of the pileus. The newest elements are always the smallest. These occur nearest the stem where they are also the most crowded. As the palisade layer passes outward into the primordium the elements appear to be less crowded, more irregular, and larger in diameter. The primordium of the hymenophore gradually passes into pileus margin, where the hyphae are strongly hyponastic and grow irregularly into the blematogen over the stem (fig. 67).

ABSENCE OF MARGINAL VEIL.—As the interstitial growth of the hyphae pushes the margin of the pileus outward, the gill cavity becomes larger and larger, and in consequence the blematogen, which lies between the pileus and stem, is constantly reduced. Whatever fibrils or scales are left on the margin of the pileus are remnants of this. No instance could be found which showed clearly any additional growth of fibers from the margin of the pileus or from the stem into the fundamental tissue which lies between these two regions. The pileus margin is strongly hyponastic and its hyphae, curving downward and inward, grow into the blematogen, but do not reach completely across to the stem (figs. 11, 31, 56, 61, 67, 74, 77, 79). The delicate cobwebby fibrils, which cover the gill cavity in young buttons and usually rupture very early (fig. 65), are evidently of blematogenous origin. In the forms studied here there is no marginal veil in the sense of ATKINSON, who considered it a structure at least in part "sui generis" (**2, 3**). This condition is what we should naturally expect, as one of the characteristics of the genus *Inocybe* in the systematic works is the absence of a marginal veil. By the time the period of vigorous lateral expansion of the pileus is reached, scarcely a trace of the blematogen remains (fig. 65).

DEVELOPMENT OF GILLS.—The gills develop in exactly the same manner as has been described previously for all endogenous forms (excepting those of the *Amanita* type), very careful and detailed accounts of which may be found in ATKINSON's later papers (**6, 7**).

As has been shown, the pileus begins its development at the stem and gradually extends its organization into the hymenophore primordium at the margin of the pileus (fig. 67). Growth continues to be centrifugal. The gill ridges start to develop at the stem in regular spaced areas and radiate outward toward the margin. On account of the very great density of the palisade elements and the continuous addition of new fibers by branching of the palisade elements, the surface of the latter is soon thrown out into folds (figs. 18, 38, 66). Multiplication of hyphae nevertheless continues to go on, and with it certain elements in the layer subjacent now begin to elongate rapidly and to carry downward the much crowded palisade layer. Since the growth of these young salients begins at the stem, the gills elongate first in this region. Passing outward the ridges become less developed until they disappear in the even palisade surface (figs. 7–10, 26–30, 42–46, 56–60, 67). Elongation of the elements of the trama continues while the ridges are progressing outward until mature gills, extending from the stem to the pileus margin, are fully developed. As these radiating rows get farther and farther apart, secondary gills form in the same manner between them. Before the basidia mature, certain elements of the palisade layer push out very rapidly and form cystidia (figs. 49, 68, 69), the nucleus of one of which shows plainly in fig. 49. Successive stages in the development of young gill salients are shown in the high-power photographs of *I. entheloides* (figs. 50–52). Occasionally the gill cavity is strongly arched,[3] and the development of the ridges appears to begin on the stem, a circumstance which brings about appearances such as are shown in figs. 43 and 44 in sections cut parallel to the medium axis. In consequence the salients here are cut nearly perpendicular to their direction of growth, and the gill cavity which extends in between them appears as a series of little pockets. A similar appearance at the margin is often caused by cutting perpendicular to the salients on the enrolled edge of the pileus (figs. 14, 15, 34, 64). The development of these plants was not carried beyond the stages represented in figs. 49, 68, and 79, in which well developed cystidia,

[3] See ATKINSON (**6, 7**) for a complete explanation of these appearances.

but as yet only primordia of basidia and paraphyses, had formed on the half mature gill salients.

Summary

1. Basidiocarps are developed from young buttons of fundamental tissue, within which is organized a growing region of very densely interwoven hyphae of small diameters. By progressive growth the stem is first formed, and later, at the stem apex, the pileus fundament, while the ground tissue on the outside becomes the blematogen or universal veil. No marginal veil is formed. The blematogen is finally completely lost or becomes concrete with the pileus.

2. The gills develop as previously described for forms of the Agaricaceae (not of the *Amanita* type). In the furrow between the pileus and stem fundaments a dense irregular hymenophore primordium is formed, which is soon replaced by an even palisade layer. Crowding of the elements in the palisade layer, due to excessive branching, causes the surface to be thrown outward into folds, which are then carried downward by the elongation of hyphae of the layer subjacent to them. The ridges develop from the stem centrifugally in regular radial rows. Later secondary gills form in a similar manner between them.

In conclusion I wish to express my appreciation to Professor W. W. ROWLEE for his kindness in allowing me the use of the photographic apparatus in the College of Arts and Sciences.

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EXPLANATION OF PLATES XVIII–XXII

FIGS. 1–15, 21–34, 39–46, 53–65, 68, 70–81 were taken with a Zeiss horizontal camera and a Spencer Lens Co. 16 mm. objective; the others were photographed by means of a Bausch & Lomb vertical camera and Zeiss lenses.

PLATE XVIII

Inocybe obscura

FIGS. 1, 2.—Median sections of two young fruit bodies, showing differentiation within blematogen of stipe and pileus fundaments; ×34.

FIGS. 3, 4.—Median and tangential sections of older basidiocarp in which hymenophore primordium and gill cavity have appeared; ×34.

FIGS. 5, 6.—Median and tangential sections of fruit body, showing palisade layer; ×34.

FIGS. 7–10.—Series of median and tangential sections of a fruit body in which young gill salients have appeared; ×34.

FIGS. 11–15.—Median and tangential sections of older fruit body, showing gills more strongly developed; fibrillose hyphae from pileus have replaced blematogen; ×34.

FIGS. 16, 19.—Details from figs. 4 and 3 respectively, showing hymenophore primordium; ×158.

FIGS. 17, 20.—Details from figs. 6 and 5 respectively, showing crowded palisade layer previous to formation of gills; ×158.

FIG. 18.—Young gill salients; detail from fig. 9; ×158.

PLATE XIX

Inocybe infelix

FIG. 21.—Median section of young fruit body, showing organization of stem, pileus, and hymenophore fundaments within blematogen; ×34.

FIGS. 22, 23.—Median and tangential sections of slightly older basidiocarp in which gill cavity has appeared; ×34.

FIGS. 24, 25.—Median and tangential sections of fruit body in which palisade layer is developing; ×34.

FIGS. 26–30.—Median and tangential sections of fruit body in which gills are beginning to form; ×34.

FIGS. 31–34.—Series of sections from older fruit body with developing gills; ×34.

FIGS. 35, 36.—Details from figs. 22 and 23 respectively, showing hymenophore primordium; ×240.

FIG. 37.—Detail from fig. 25, showing palisade layer; ×240.

FIG. 38.—Detail from fig. 28, showing young gill salients; ×240.

PLATE XX

Inocybe eutheloides

FIG. 39.—Young button in which pileus and stem primordia are outlined within loose blematogen; ×34.

FIGS. 40, 41.—Median and tangential sections of older fruit body, showing growth of pileus into blematogen layer and hymenophore primordium; ×34.

FIGS. 42–46.—Median and tangential sections of fruit body in which gills are forming; ×34.

FIGS. 47, 48.—Details from figs. 40 and 41 respectively, showing hymenophore primordium; ×158.

FIG. 49.—Section of gills of more mature fruit body, showing developing cystidia; ×158.

FIGS. 50–52.—Series of sections from fruit body of figs. 42–46, showing successive stages in formation of gill ridges; ×158.

PLATE XXI

Inocybe hystrix

FIG. 53.—Young button, showing fundamental tissue into which stem primordium is advancing; ×34.

FIGS. 54, 55.—Median sections of two fruit bodies in which pileus fundament is advancing into blematogen; ×34.

FIGS. 56–60.—Series of longitudinal sections, showing development of gill salients; ×34.

FIGS. 61–64.—Series of sections from slightly older fruit body; ×34.

FIG. 65.—Median section from nearly mature fruit body in which pileus has begun to expand; ×34.

FIG. 66.—High power photograph from fruit body of figs. 56–60; ×158.

FIG. 67.—Detail from fig. 61, showing progressive differentiation of hyphae from primordial hymenophore into pileus margin; ×158.

FIG. 68.—Tangential section of fruit body of fig. 65, showing developing cystidia; ×34.

FIG. 69.—Detail from fig. 68; ×158.

PLATE XXII

Inocybe geophylla

FIG. 70.—Longitudinal sections of young buttons; ×34.

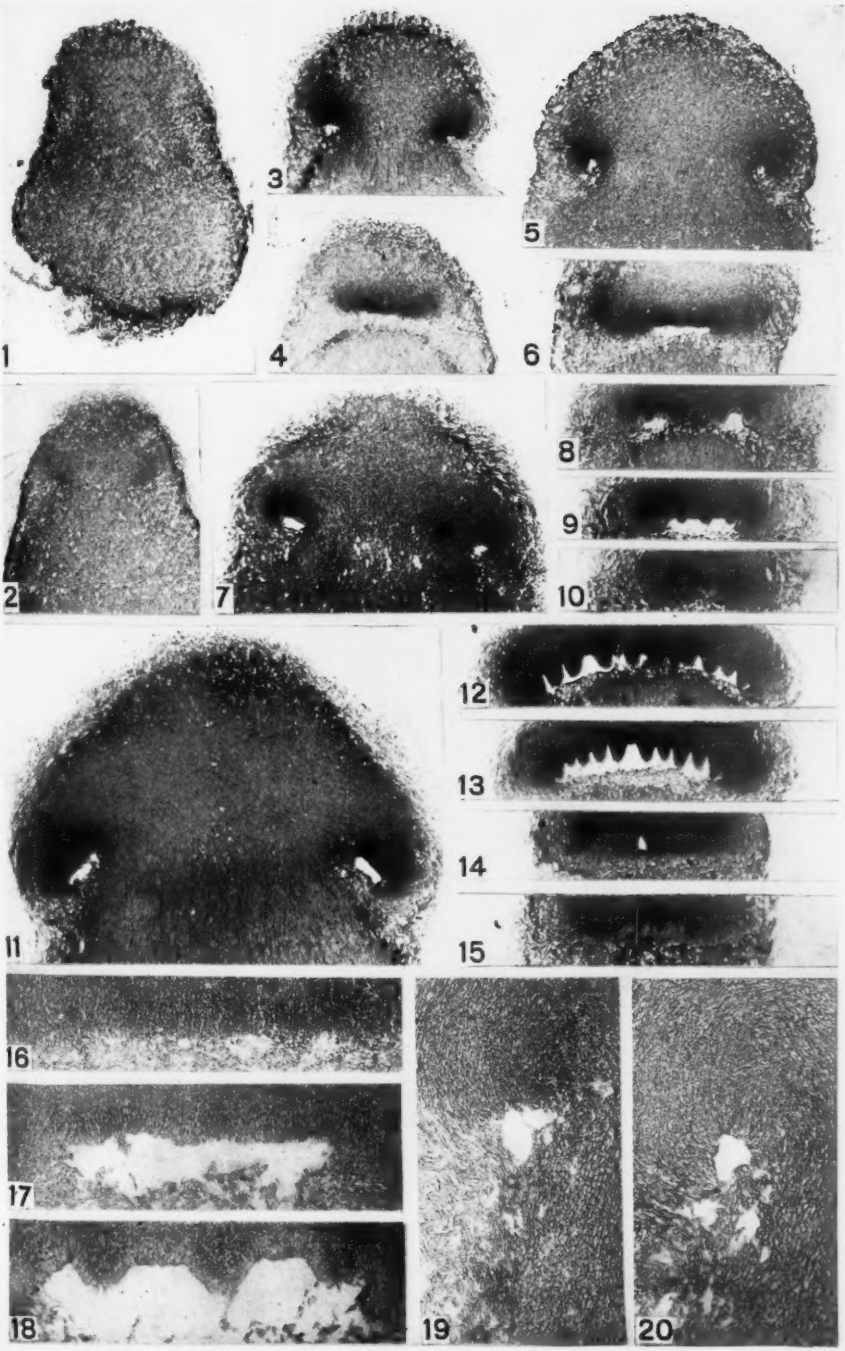
FIG. 71.—Median section in which pileus and stem fundaments are outlined within a 2-layered blematogen; ×34.

FIGS. 72, 73.—Median and tangential sections of fruit body in which primordium of hymenophore is appearing; ×34.

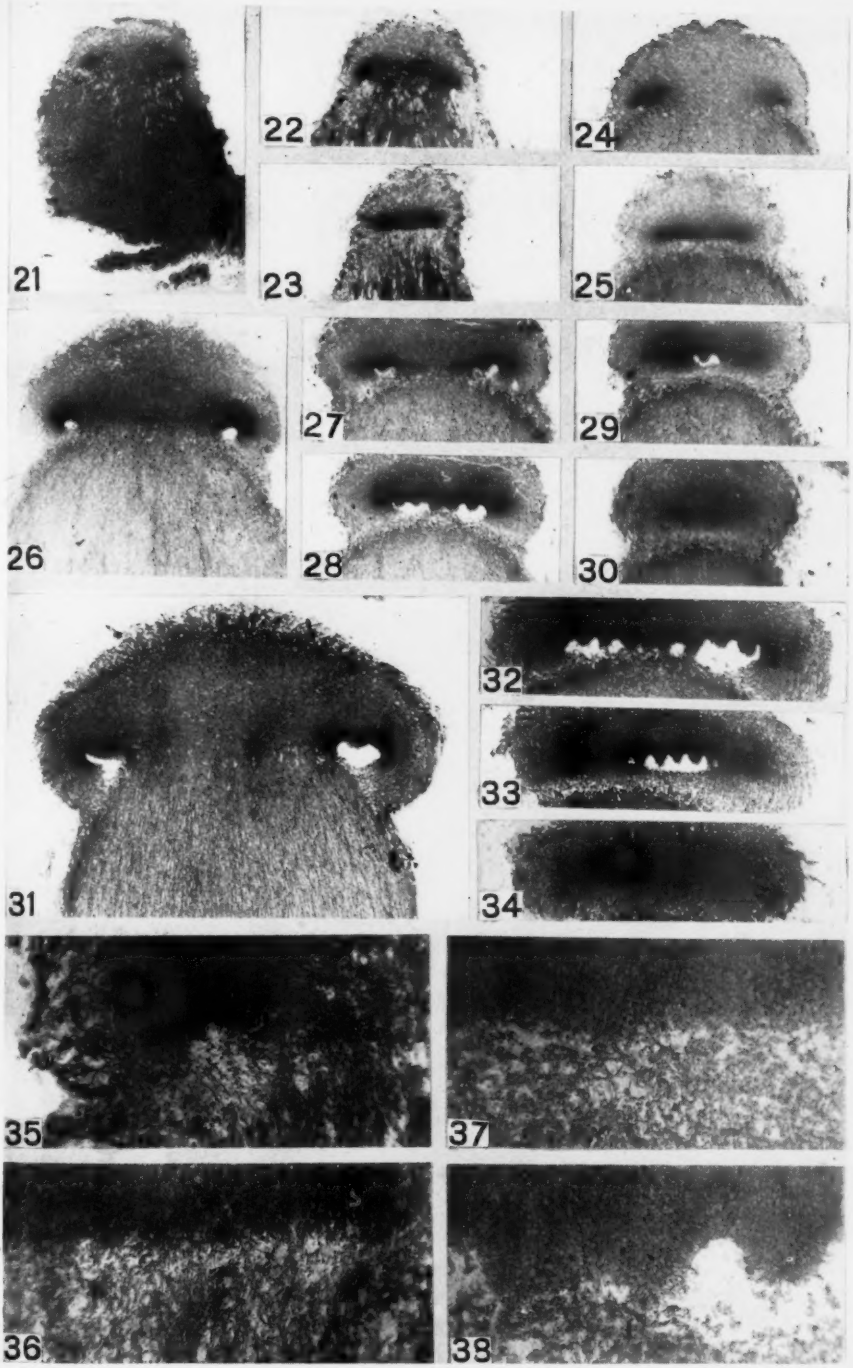
FIGS. 74–76.—Median and tangential sections of older fruit body in which palisade layer has become organized and first gill salients are appearing; ×34.

FIGS. 77, 78.—Median and tangential sections of older fruit body; ×34.

FIGS. 79–81.—Older fruit body in which gills are nearly mature and on which cystidia have developed; duplex universal veil still present over whole fruit body; ×34.



DOUGLAS on INOCYBE



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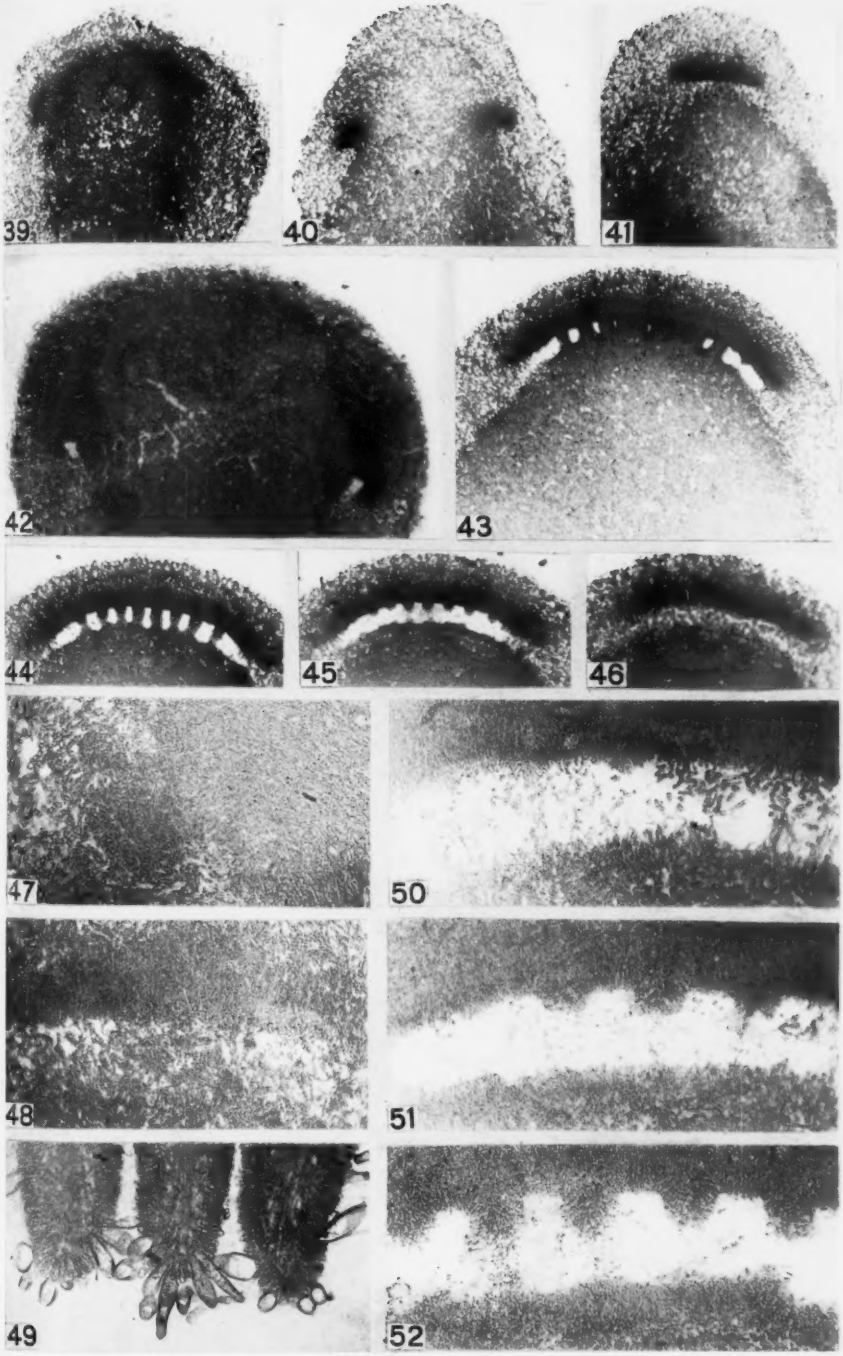

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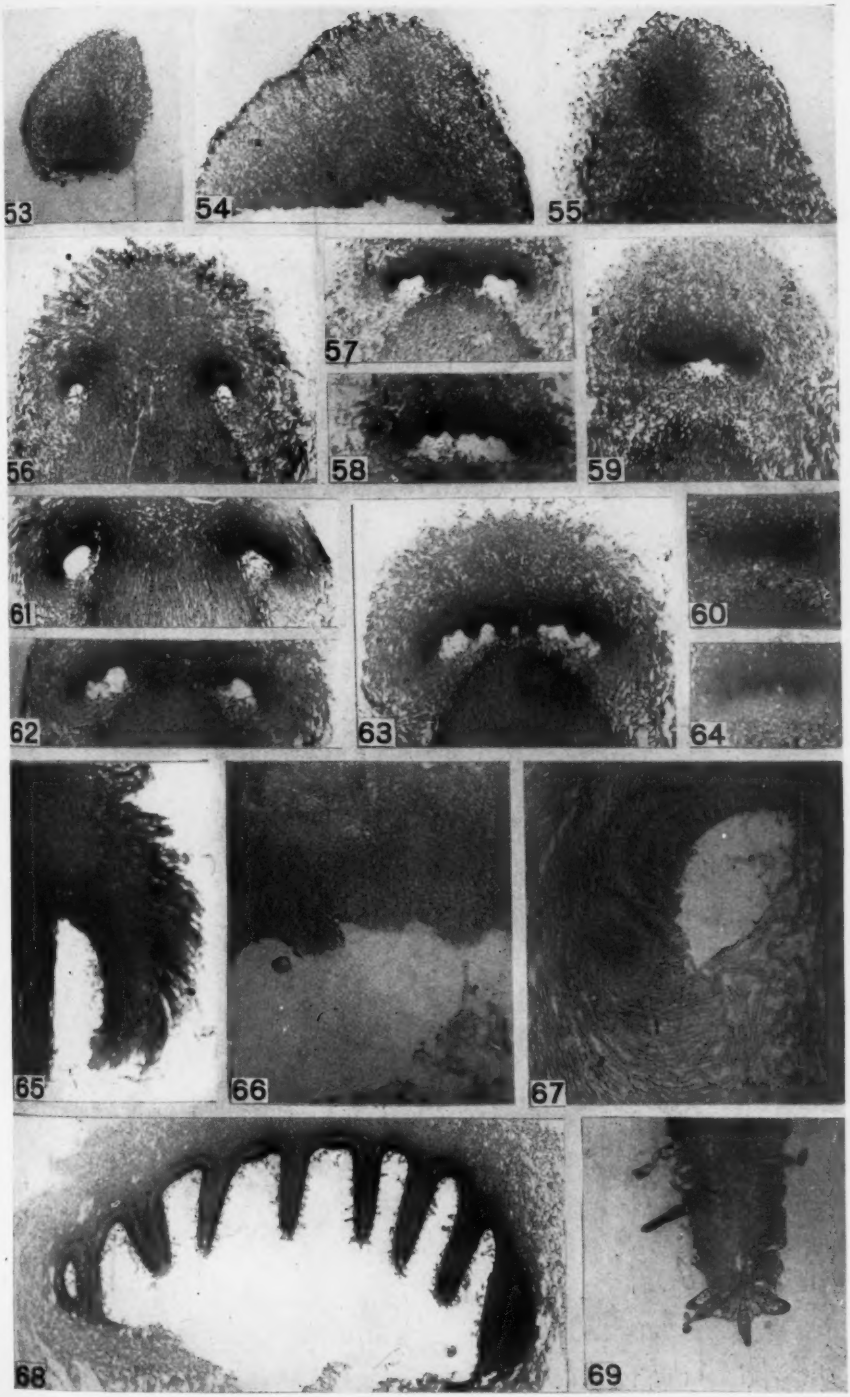

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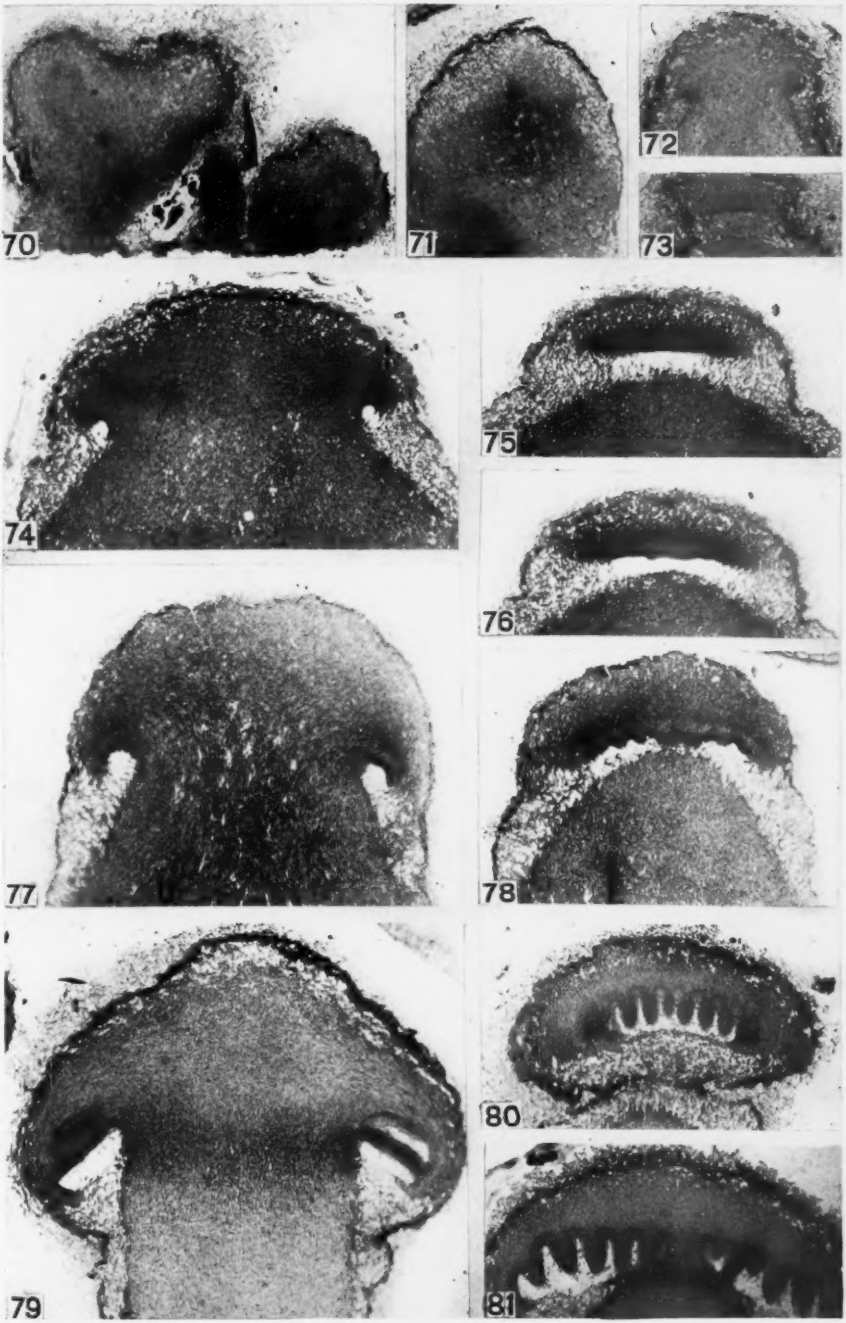

DOUGLAS on INOCYBE

PECTIN RELATIONS OF SCLEROTINIA CINEREA[1]

J. J. WILLAMAN

The pectic substances which constitute the middle lamellae of fleshy fruits, and thus serve as the cementing material between cells, are of great interest to the plant pathologist because of the fact that if an invading organism is to make its way into a tissue, it must either pass along the line of the middle lamella *between* the cells, or it must bore *through* the cells. In the first case a pectic enzyme at the hands of the parasite may be presupposed, and in the second case a cellulose enzyme.

The mechanism of infection by *Sclerotinia cinerea* has received particular attention recently by COOLEY (4) and by VALLEAU (8). COOLEY maintains that its hyphae in plum tissue are mainly intracellular; while VALLEAU finds them to be entirely intercellular, and produces photomicrographs to prove it. COOLEY could not demonstrate the presence of an enzyme which would dissolve the calcium pectate of the middle lamella. He also failed to find any evidence of a softening of the tissue in advance of penetration. VALLEAU, by more careful methods, noticed a marked separation of the cells in rotted tissue, and demonstrated that an extract of rotted apple would bring this about. The agent in this case is the enzyme designated by VALLEAU "pectinase," but more correctly called "pectosinase" according to the terminology of its discovery (3, 10), and of ATKINS (2). VALLEAU's illustrations show that it is secreted considerably in advance of the penetrating hyphae. The question of oxalic acid being the solvent was considered by both writers. COOLEY found appreciable amounts of the acid in rotted peaches and plums, but was not convinced that it was the middle lamella solvent. VALLEAU demonstrated that dilute solutions of oxalic acid would soften the tissues of these fruits, but not of potato, which facts convinced him that this acid is not the only factor involved in the disintegration of the middle

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lamella. Both writers agree that *Sclerotinia* is more virulent on ripe than on green fruit, because in the ripe fruit the middle lamellae are disintegrated and allow easier penetration.

COOLEY found that the fungus coagulates soluble pectin, even when calcium is presumably absent from the medium, and that it does not dissolve precipitated "calcium pectinate" suspended in an agar nutrient medium. As to the question whether any pectic material is assimilated by this fungus, HAWKINS (**6**) found no diminution in the pentosan content of peaches which had been rotted by it, and COOLEY's observation that it could not grow on "calcium pectinate" would indicate failure to assimilate this pectic material, at least.

The present status of the question of pectin relations of *Sclerotinia cinerea*, therefore, is that it disintegrates the tissues by dissolving the middle lamella with a secreted pectosinase, and probably also with oxalic acid. What disposition is made of the dissolved pectic material, and what function the pectase serves, have not been suggested. The fungus also coagulates soluble pectin by means of pectase. Pectinase (see later for definition) has not been demonstrated.

During the course of some work on *Sclerotinia* the writer (**9**) made several interesting observations on the behavior of this fungus toward the various pectic substances. These are recorded in the following notes.

Assimilation of pectin

Before recounting the observations made on the pectic relations of this fungus it might be well to explain the nomenclature that has been adopted in this paper. It is the same as that used by ATKINS (**2**). Pectosinase is the enzyme that dissolves the middle lamella, with the formation of soluble pectin. Pectase coagulates soluble pectin to a gel in the presence of a calcium (or barium or strontium) salt. Pectinase hydrolyzes soluble pectin, and also the gel formed by pectase, to reducing sugars. Such definite names have not been given to the various pectic products; hence the particular one in question in any particular case can be told only by the context.

In order to test the assimilatory power of *Sclerotinia* toward soluble pectin, a sample of the latter was made by precipitating prune juice with alcohol, reprecipitating twice, and then drying in an oven and grinding. The resultant powder was incorporated in a mineral nutrient medium to the extent of 0.4 per cent. With no sucrose added, growth took place, but only about one-fifth as rapidly as when some sucrose was present. Whether this growth was due to the assimilation of pectin, or to sugars adsorbed during the preparation of the pectin, was not evident, since no analyses were made. To test this point quantitatively, another preparation of pectin, from peach, was made. It was decided to follow the product by analyzing for its content of pentosan. Although this is open to many objections, the chief of which is the questionable accuracy of the existing methods of pentosan determination, no other way of studying the fate of the pectin in media appeared feasible. The official (1) phloroglucide method was used. The pectin preparation showed a content of 15.0 per cent furfural, or 25.6 per cent pentosan. SCHRYVER and HAYNES (7) obtained 18.6 per cent furfural in turnip pectin. They had a far purer preparation, however, than the writer attempted to obtain.

A medium containing mineral salts and 2 per cent of pectin was prepared, and two Erlenmeyer flasks, each with 50 cc. of medium, were sterilized and inoculated with spores of the fungus. Growth was slow but typical. The medium became a gel, due to the coagulation of the pectin by the fungus. After three weeks the colony in each flask had attained a diameter of 3.5 cm. (see 9 for the writer's method of estimating the growth of this fungus). By this time also the gel had become almost completely liquefied, and the liquid portion gave no precipitate with alcohol. The colonies were carefully removed, freed from the adhering gel of the medium as well as possible, and then the two mycelia and the two media combined for analysis. The results were as follows:

Pentosan in original media	0.502 gm.
Pentosan in mycelia of culture 572	0.014 gm.
Pentosan in residual media	0.040 gm.

Thus a total of 0.054 gm. of pentosan remained in the culture flasks at the end of the period of growth, whereas 0.502 gm. was

present in the pectin at the start. Very evidently during the growth of the fungus the pectin was assimilated in part, at least. About nine-tenths of the furfural-yielding material of the pectin had disappeared. Presumably this material was utilized by the fungus for energy, but was not stored in any appreciable quantity in the hyphae. It is possible that the small amount found in the latter was due to pectic gel enmeshed in the hyphal weft.

The course of the changes involved when *Sclerotinia cinerea* grows on a pectin medium may be outlined as follows. There is first a coagulation of the soluble pectin to a gel by means of pectase, followed by a slow liquefaction of the gel during the progress of the growth of the fungus. This liquefaction is accompanied by an assimilation of at least the furfural-yielding constituents of the pectin. The fungous hyphae contain very little if any furfural-yielding bodies. It is not known whether the enzyme pectinase is involved in the liquefaction of the calcium pectate. Presumably it must be present in order to liberate soluble split products from the gel before the latter becomes available to the hyphae, although this point has not been demonstrated.

HAWKINS, on comparing the analyses of peaches before and after rotting by *Sclerotinia cinerea*, found no appreciable change in the pentosan content. This may or may not be evidence contrary to the preceding. In the whole fruit there is an abundance of carbohydrate food other than the pectin, which the fungus can utilize far more readily. As already stated, growth on the pectin medium was very slow, indicating that the fungus can utilize pectin, but with difficulty; hence it is fair to believe that in the presence of abundant sugars in a natural host the pectins are probably not drawn upon for nutrients.

Secretion of pectase

Whenever *Sclerotinia* is grown on a fruit juice medium containing soluble pectin, the latter is coagulated to a gel. This gel may vary in extent from a few suspended flocs to a solid medium, depending on the amount of pectin present. The gel is insoluble in hot water. It dissolves readily in dilute alkali and in dilute acid, and is reprecipitated from these solutions by alcohol. It is

soluble in ammonium oxalate, with the concomitant formation of crystals of calcium oxalate. In accordance with the usual nomenclature (**2, 5, 10**), therefore, the coagulum is judged to be calcium pectate, and its formation to be brought about by the enzyme pectase, secreted by the fungus. COOLEY demonstrated a similar pectic enzyme, differing from the present one, however, in that it brought about the coagulation in the supposed absence of calcium. He designated his enzyme pectinase, but that is merely a question of nomenclature. As regards the necessity for the presence of calcium, it is possible that the pectin preparation used by COOLEY contained some of this element, brought down during the alcoholic precipitation. He states that a preliminary test of the plum juice with oxalic acid showed the absence of calcium, and that this treatment was therefore abandoned as unnecessary. It is inconceivable that a fruit juice should contain no calcium whatever; hence it is very probable that the pectin coagulated by alcohol did contain some calcium, since the latter is a characteristic constituent of the alcholic precipitate of all plant juices.

In order to determine to what extent pentosans are present in the mycelium of *Sclerotinia*, either as enmeshed pectic gel or as an actual constituent of the fungous body, a few analyses were made of felts grown on various media. The felts were removed from the media, carefully washed with water, dried between filter paper, and then placed in a desiccator over quicklime. When perfectly dry they were ground to a powder, sampled, and analyzed. The following data were obtained, expressed as percentage of pentosan in the dry mycelium:

No. 568. Grown on synthetic sucrose-salts media entirely free from pectin and pentose; sporulation abundant ..... 3.5 per cent pentosan

No. 569. Grown on whole prune juice, pectin fairly abundant; sporulation moderate ..... 1.5 per cent pentosan

No. 570. Grown on whole peach juice and apricot juice, pectin abundant; sporulation abundant ..... 0.8 per cent pentosan

No. 572. Grown on the prepared pectin medium described; sporulation absent ..... 3.9 per cent pentosan

That the figure obtained in no. 568 actually represents the pentosan content of the mycelia is doubtful. When the phloroglucin was added to the furfural-containing distillate, a bright red

color developed, which gradually changed to a reddish brown precipitate. The normal color change is a green solution at first, changing to a black precipitate. It is possible that the fungus yielded during the acid distillation some substance other than furfural which reacted with the phloroglucin. Furthermore, the media in this case contained no pentose substances whatever; hence it is very unlikely that the fungous bodies would produce more furfural-yielding materials here than in the other cases, where the possibilities of enmeshed pectin were present. The high value for no. 572 is explainable by the fact that the felt grew on a firm gel of calcium pectinate, making it difficult to obtain a clean separation of mycelium from medium in preparing the samples for analysis.

From these data it is evident that only a very small amount of pentosan is present in the felt of *Sclerotinia cinerea*, either as enmeshed pectin or as a constitutional substance. Whether the latter actually exists is not proved by the data. Furthermore, microchemical tests failed to show pectic substances in any portion of the hyphae.

A possible function of the enzyme pectase in a fluid medium, such as fruit juice, is suggested when the characteristics of the growth of *Sclerotinia* on such a medium are taken into consideration. These juices always contain soluble pectin; they also contain some calcium, but there is never any formation of calcium pectate without the presence of the fungous hyphae. As soon as the germinating spores in these media have begun to form a slight weft, this weft can be lifted from the medium with a mass of gelatinous material clinging to it. In fact, the young felt consists of a relatively small mass of hyphae imbedded in a large mass of the gelatinous coagulum. This coagulum can be removed by gentle pressure through cheesecloth in the case of young felts. As they grow older, however, the hyphae increase in bulk, become closely packed together, and the coagulum loses water and becomes firm and slippery. A mature sporulating felt consists typically of three layers: an upper white layer of loosely packed hyphae bearing the sporophores; a middle layer of black, leathery, closely packed mycelium; and a lower layer consisting of a few hyphae and the concentrated

pectin coagulum. The lower layer merges into the loose coagulum of the medium, and most of it easily sloughs off when the felt is washed in water. When an apple juice rather high in pectin is used, the whole mass becomes a rather soft gel within a few days. This gel enables the fungus to build up a semi-solid medium upon which to support aerial hyphae and sporophores.

The possible function of pectase to the fungus when invading a host tissue offers a subject for speculation, at least. The substance of the middle lamella is usually spoken of as calcium pectate. That it is the same substance as the calcium pectate gel formed by pectase is rather doubtful (**2, 5**). The work of various investigators has proved conclusively that this fungus dissolves out the middle lamella, either by the enzyme pectosinase or by oxalic acid. If it be oxalic acid, the calcium of the middle lamella would be removed as insoluble calcium oxalate, leaving a pectin residue, presumably soluble, or at least no longer capable of cementing the cell together. Whether *Sclerotinia* has the power of forming a calcium pectate gel out of such pectic residue is not known, since the nature of this material is not determined. If, however, the solution of the middle lamella be brought about by pectosinase, we have a different case to consider. We really know nothing definite concerning the action of this enzyme on the middle lamella, but presumably some simpler pectic substance would be formed along with a soluble calcium complex. The fungus would penetrate the dissolved substance of the lamella, and then reprecipitate it, presumably as the calcium pectate found in the apple juice cultures. Since it is not known whether the pectin obtained by boiling a ripe fruit in water is the same as the pectin produced by the action of pectosinase on the middle lamella, we are perhaps not entirely justified in assuming that the same substance is formed by pectase acting on dissolved middle lamella *in vivo* and on soluble pectin in an extracted fruit juice. The work of previous investigators, however, gives us good reason to believe that the pectic gels in the two cases are very similar, if not identical (**2, 5, 10**).

Given this hydrophyllic gel, what purpose may it serve the invading parasite? VALLEAU believes that the reason *Sclerotinia*

produces a firm and not a soft rot of plums is that its comparatively large hyphae completely fill the intercellular spaces produced by the collapse of the cells, and that thus the tissue retains its shape and firmness, even after rotting. The writer believes it much more probable that the laying down of considerable calcium pectate gel maintains the firmness of the rotted tissue. This view is further supported by the evidence already stated that this fungus does not consume pectic material in its metabolism to any marked degree.

Certain advantages to the fungus can be seen in this production of calcium pectate gel. Since a fruit, rotted on the tree by this fungus, typically retains its form and turgidity for some time, the fungus is enabled to sporulate (chlamydospores in this case) copiously for several days, during a period when the tree is full of ripe fruit susceptible to the rot. Again, many of these rotted fruits do not drop from the tree; they slowly shrivel up, usually without any break in the skin, and form the characteristic mummies of plum and peach orchards. The following spring these mummies imbibe water readily, due in great part to the strongly hydrophyllic calcium pectate gel, and again sporulate profusely. After this the mummies drop to the ground and remain dormant for a year, when they again imbibe water, and produce an abundance of ascospores at the time of blossoming of the fruit trees.

Summary

Sclerotinia cinerea, when grown on a fruit juice containing soluble pectin, coagulates this pectin to a gel of calcium pectate by means of the enzyme pectase. When simple sugars are available, the fungus does not assimilate pectic substances. When, however, pectin alone is available, it is slowly assimilated. The mycelium contains no pectic substances, except such as occur in particles of calcium pectate gel enmeshed by the hyphal filaments. When the fungus invades a tissue, it follows the line of the middle lamella by dissolving out the latter with the enzyme pectosinase. It probably reprecipitates the pectin of the lamella as calcium pectate. The latter, being a hydrophyllic gel, maintains the firmness of the fruit even after rotting, which is a characteristic of fruit rotted by *Sclerotinia*. This highly imbibing gel is probably also

of service to the fungus at subsequent periods by aiding the organism in acquiring a water supply. The production of pectinase is postulated but not demonstrated.

Dr. SOPHIA H. ECKERSON, of the University of Chicago, very kindly assisted the writer in the microchemical examination of the mycelia for pectin.

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CARBON MONOXIDE A RESPIRATION PRODUCT OF NEREOCYSTIS LUETKEANA

SETH C. LANGDON AND W. R. GAILEY

(WITH THREE FIGURES)

The consideration of carbon monoxide as a plant respiration product is somewhat novel from the point of view of the plant physiologist. That such may be the case seems clear from the evidence to be submitted in this paper. This investigation was carried on during the summer of 1918 at the Puget Sound Marine Station at Friday Harbor, Washington. It was expected to continue the investigation for another summer before publication. This was not possible, however, and since it now appears wholly unlikely that the work will ever be carried further by the authors, the data at hand are presented.

In previous papers by LANGDON,[1] it was shown that there was present an average of 4 per cent (by volume) of carbon monoxide in the pneumatocyst of the giant Pacific Coast kelp, *Nereocystis Luetkeana*. This statement was based on the analysis of the gas from about 1000 different specimens. The quantity of carbon monoxide varied from 1 to 12 per cent, the average being 4 per cent. The actual existence of the carbon monoxide in the gas from the kelp was demonstrated by a variety of chemical tests, by its physiological effects on animals, and by the standard spectroscopic blood tests. There was also present in the gas 15–25 per cent of oxygen, the remainder of the gas being nitrogen. There was no evidence of the presence of other gases, except, of course, water vapor, although particular search was made for carbon dioxide, hydrogen, and hydrocarbon gases.

The occurrence of carbon monoxide within a living plant at once raised the question as to its source and possible relation to anabolic or katabolic processes. In the theoretical[2] considerations

[1] Jour. Amer. Chem. Soc. **39**:149. 1917; also Puget Sound Marine Sta. Publ. **1**:237. 1917.

[2] SPOEHR, H. A., Plant World **19**:1. 1916.

of the mechanisms of photosynthesis, carbon monoxide has often been considered as an intermediate step in the reduction of carbon dioxide, especially since it is so closely related chemically to formaldehyde and formic acid. Heretofore there has never been any evidence of the existence of free carbon monoxide within a living plant. The possibility of its formation by enzyme action or by decay processes was early suggested, and was the first point investigated. Finely ground kelp was allowed to undergo autolysis in contact with sea water, and the gases evolved were examined. No carbon monoxide was formed, but the gas consisted almost entirely of carbon dioxide and hydrogen.

The next step was to determine how rapidly carbon monoxide was formed within the living plant. The method of work and the further discussion will be made more clear if prefaced by a brief description of *Nereocystis*. Fig. 1 shows the kelp as it lies normally, almost submerged in the sea water, anchored to the rock bottom and supporting the streaming fronds from the top of the hollow gas-filled stipe. The plants vary greatly in size. Individuals are often 80–100 ft. in length, and contain several liters of gas which is usually at reduced pressures.[3] The inside of the gas cavity is relatively dry, and is lined with a delicate weblike structure called sieve tubes. The plant will withstand a great deal of mutilation and still continue to live and grow, if kept in sea water.[4]

It was found practicable to cut off the lower part of the stipe and in the upper part to substitute a gas of known composition for that normally present in the pneumatocyst. The cut end was closed by a cork stopper, and the plant weighted and submerged in the sea, tied to a floating support, as shown in fig. 2. After a suitable interval, changes in the gas composition were determined by analysis. In the first experiments tried, primarily to determine the rate of formation of carbon monoxide, air was substituted for the kelp gas. This was accomplished by filling the cut stipe with sea water and then emptying. This process repeated three or four times removed the small bubbles that tended to adhere to the delicate sieve tube lining of the pneumatocyst, and insured the

[3] FRYE, T. C., Puget Sound Marine Sta. Publ. 1:85. 1916.

[4] FALLIS, A., Puget Sound Marine Sta. Publ. 1:1. 1916.

complete removal of all the gas originally present. The cut end of the now air-filled stipe was corked and anchored at the surface of the sea as previously described.

FIG. 1

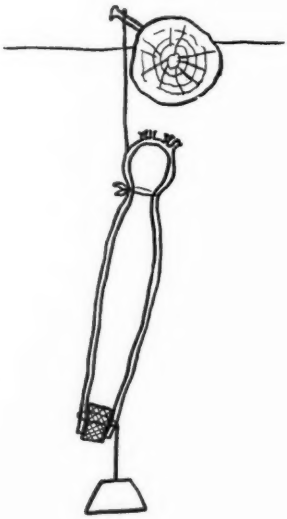

FIG. 2

Analysis of the gases from a series of these cut and air-filled plants was made after various intervals of submergence. The typical data given in table I show clearly the gradual formation of carbon monoxide, accompanied by the appearance of carbon dioxide, which latter was undoubtedly due to decay processes,

since carbon dioxide is not found in the gas normally present within the kelp. In general, the cut and corked sections of stipe remained sound enough to be tight for a week or ten days, although evidence of local decomposition was apparent. This production of carbon monoxide, when the stipe was filled with air, was confirmed by many determinations with different specimens. In most cases it appeared in quantities as great as 1 per cent or more. The presence or absence of the fronds had no relation to the carbon monoxide formation. Carbon monoxide was produced by sections cut from any part of the hollow stipe, filled with air, corked, and similarly suspended in the sea. Even the round bulblike top of the stipe,

TABLE I

Time	Percentage CO_2	Percentage CO	Percentage O_2
Start	0.0	0.0	20.8
24 hours	0.3	0.0	16.5
48 hours	0.0	0.4	13.0
73 hours	0.6	1.0	7.0
97 hours	1.0	3.2	6.2
110 hours	1.1	4.5	5.0

devoid of fronds, would form it almost as readily as if practically the whole of the plant were used.

Two other methods of displacing by air the gas originally contained within the kelp were used, but gave no difference in the final results. The first of these was to insert a rubber tube at the cut end, so that it extended the whole length of the stipe and up into the bulblike top; then to force in through the tube a large quantity of air, and thus sweep out all of the kelp gas. The other method was to draw the original gas out by connecting the cut end to a good suction filter pump. Alternately evacuating and filling with air served to accomplish the desired substitution without getting the inside of the gas cavity wet. It would be interesting to make the substitution under strictly aseptic conditions, but this the authors were not able to do.

Since carbon monoxide was formed in quantity in the living plant within a few days and was not formed by decay or autolysis, it might have been formed either as a product of respiration or as

an intermediate step in photosynthesis. If the latter, it should not appear if the experiments were carried out in the dark. To test this, boxes were constructed which were light-tight, but which would allow a ready flow of water through them. These boxes were 1 ft. square and 18 ft. long. The ends were closed by light traps, the baffle boards of which were inclined in the direction of flow of the water (fig. 3). The lids were also light-tight. All

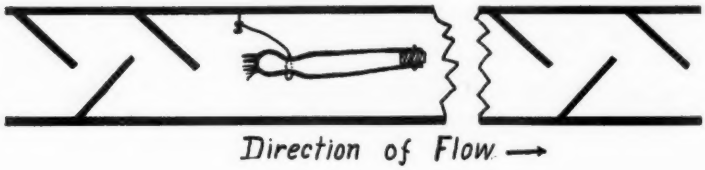

FIG. 3

holes and cracks were closed with pitch, and the whole interior painted a dead black. The boxes were weighted so as to just float; the waves washed entirely over them except when the water was perfectly calm. The boxes were anchored in the bay (Friday Harbor, Washington) where the tidal currents are heavy, so that there was practically always a flow of water through the boxes. The boxes were large enough to hold several specimens without impeding the flow of water.

In the first experiments, the top 18 inches of stipe from 10 kelps were filled with air by displacement with sea water and corked and placed in the dark boxes. Half of them had the fronds removed. After 5 days in the dark they were removed and the gas analyzed. All showed carbon monoxide. The range was from 0.4 to 1.7 per cent, with an average of 0.7 per cent. The 20.9 per cent of oxygen in the air with which they had been filled had practically disappeared, and there was about 4 per cent of carbon dioxide. The oxygen was used by respiration and decay processes. These data were checked by extended experiments, and it was made certain that in the dark as well as in the light carbon monoxide was formed regularly in the air-filled section of the stipe, and that there was no relation between its appearance and the presence or absence of the fronds.

The appearance of CO_2 and the lowering of the oxygen content when the unmutilated plants were kept in the dark for some time were shown by the following experiments. Twelve whole plants were gathered from the same bed, precaution being taken to avoid in any way disrupting the gas cavity. The gas from 6 of them was analyzed at once and showed an average of 15 per cent of oxygen, 3.2 per cent of carbon monoxide, and no carbon dioxide. The other 6 plants were placed intact in the dark boxes, and after being anchored out in the tidal currents for 6 days showed the following average gas composition: oxygen 4.7 per cent, carbon monoxide 2.9 per cent, and carbon dioxide 0.5 per cent. There was therefore a marked decrease in the oxygen content, and an appearance of carbon dioxide which is practically never present in the kelp when freshly collected, while there was practically the same carbon monoxide content.

The substitution of gases other than air for those normally present was next undertaken. As a result of more than 40 carefully made experiments, in which nitrogen was substituted for the kelp gas, it can be stated confidently that no carbon monoxide was formed, either in the light or in the dark, either when fronds were present or when they had been removed, or at any intermediate time between the initial filling and the 8–10 days before decay had become so pronounced that observations could no longer be made. It should be remarked that a small percentage of carbon dioxide was generally formed, even though there was no oxygen present.

The nitrogen was prepared in three ways. One method was by heating a mixture of concentrated aqueous solution of sodium nitrite and ammonium chloride. The products other than nitrogen from this reaction are sodium chloride and water. The first few liters of gas evolved were discarded and the remainder showed no oxygen. The gas was washed through strong sodium hydroxide solution. The second method of preparing "nitrogen" was to absorb the oxygen from the air by means of alkaline pyrogallol. That the failure of the plant to produce carbon monoxide was not due to a trace of some unknown impurity, introduced into the nitrogen as chemically prepared and purified, was made certain by the use of nitrogen obtained by the fractional distillation of liquid

air. This nitrogen procured from the Linde Air Products Company contained a trace of oxygen, about 6–8 parts per thousand by volume, but the results obtained with it were the same as with the nitrogen prepared in other ways.

Similar experiments were carried out in which hydrogen was substituted for the kelp gas. The 15 determinations made showed no formation of carbon monoxide within 5–7 days, either in the light or in the dark. Here, as in the case of the nitrogen-filled kelp, a small percentage (1–9 per cent) of carbon dioxide was formed. It should be remarked that there was always a marked reduction in pressure for hydrogen-filled kelp. This amounts to an absorption or diffusion out of hydrogen. The whole relation of hydrogen in this connection deserves more exhaustive study.

The hydrogen used was from two sources: (1) the action of dilute sulphuric acid on the so-called arsenic free zinc; (2) a commercial product prepared by electrolysis.

A number of sections of kelp stipe were filled with a mixture of nitrogen and oxygen, both chemically prepared. The initial composition was 15.2 per cent oxygen and the remainder nitrogen. After 6 days' exposure carbon monoxide had been formed in all cases, the quantities ranging from 0.8 to 2.1 per cent. The oxygen content decreased and some carbon dioxide was formed just as in the case of the specimens filled with air. Kelp filled with a mixture containing 26.2 per cent of oxygen and the rest hydrogen showed in the same time a similar formation of carbon monoxide and a corresponding decrease in oxygen accompanied by the appearance of carbon dioxide.

The evidence so far presented seems to point to the inevitable conclusion that the carbon monoxide is a product of respiration, since it is not formed by decay or autolysis, and is formed only when there is oxygen present in the pneumatocyst.[5]

A similar supplementary series of experiments was made which supported the conclusion that the carbon monoxide was formed by a katabolic process. The gas-filled corked sections of

[5] That the CO was a respiration product was early suggested by RIGG. This conclusion was based on a special knowledge of the physiology of the plant. It was his belief that the effect was intimately related to the sieve tubes.

stipe were not put back in their normal habitat, sea water, but were left out in the air. It should be recalled that this plant will withstand a very considerable amount of desiccation and will resume growth when returned to the sea. Sections of stipe filled with air and placed in a warm, dry, dimly lighted attic developed 0.7–4.7 per cent of carbon monoxide in 5 days. The oxygen content lowered to about 4 per cent and there appeared 1–2 per cent of carbon dioxide. Similar results were obtained when specimens of air-filled kelp were placed in good daylight (not direct sunlight) or when kept exposed to the air in a dark room. Kelp filled with nitrogen or with hydrogen and allowed to stand (dry) in the air developed no carbon monoxide. On the other hand, under the same conditions, but filled with mixtures of oxygen and hydrogen, or oxygen and nitrogen, carbon monoxide was produced within a few days.

That carbon monoxide was not formed in dead kelp was shown in the following manner. A number of plants were killed by being placed for 10 minutes in sea water which was maintained at a temperature of 50° C. The stipes, full of air, were corked. Some of them were placed in the sea water in the light and some anchored out in the dark boxes. Another set similarly treated was placed in air, some of them in the light and the remainder in the dark. Analysis of the gas from the various specimens 6 days later showed no carbon monoxide. There had been a slight decrease in the oxygen content and the formation of 2 or 3 per cent of carbon dioxide. Exactly similar results were obtained when the kelp was killed by being placed in N/50 Cu SO_4 for 18 hours.

A series of experiments was started to determine what would happen if kelp were filled with oxygen-free nitrogen or hydrogen to which had been added a small quantity of carbon monoxide. These experiments were not completed, but it became clear that the change, if any, was slight.

Nereocystis Luetkeana seems to be remarkably well adapted to research on gas exchange of living cells. By the use of the very refined methods of gas analysis which are now available, some very interesting and valuable information might be gained. It is possible that traces of hydrogen or carbon monoxide not revealed

by the technical gas analytical methods used in this work may be playing important rôles in plant processes.

The gas contained in the hollow cavities of several other growing plants was investigated, but in no case was carbon monoxide found. The gas obtained from a vigorously growing garden pumpkin contained 18 per cent of oxygen with no carbon dioxide or carbon monoxide. Very similar results were obtained from the gas contained in the hollow stems of a species of *Equisetum*, the hollow stems of a species of *Petasites* (colt's foot), from the pods of green garden peas, and from the seed pod of the soft maple. In the original paper it was reported that there was no carbon monoxide in the gas obtained from the vesicles of *Egregia Menziesii*, or in that obtained from *Fucus evanescens*.

The Scripps Institute collected gas for the author from two of the southern algae. One of these, *Macrocystis pyrifera*, showed no carbon monoxide; while the other, *Pelagophycus Porra*, showed a small carbon monoxide content. These gases were collected in quart fruit jars and shipped from La Jolla, California, to Seattle, Washington, for analysis. To be definitely certain of the presence of carbon monoxide in the gas from the elk kelp, *Pelagophycus Porra*, it would be necessary to examine the freshly collected gas. It is interesting to note that *Pelagophycus Porra* is very closely related to *Nereocystis Luetkeana*, and is very similar in structure, the inside of the gas cavity of both being characterized by the presence of a pith web.

The occurrence of free carbon monoxide within a living plant is unique, so far as the authors have been able to ascertain. Its further study in relation to plant life should prove interesting, and it is not without a measure of regret that the authors leave this field to other investigators.

Summary

1. The existence of a percentage of carbon monoxide in the gas contained in the pneumatocyst of the Pacific Coast kelp *Nereocystis Luetkeana* is confirmed.

2. The substance of the kelp when ground and allowed to undergo autolysis and decay does not form carbon monoxide by enzyme action or fermentation process.

3. Kelp plants, in which the gas normally present within the floater is replaced by air, form several per cent of carbon monoxide within a few days.

4. The formation of carbon monoxide takes place only when oxygen is present as one of the gases within the floater. No carbon monoxide is formed when the floater is filled with nitrogen or hydrogen.

5. Light does not affect the rate of formation of carbon monoxide.

6. The gas obtained from the cavities of various other plants failed to show a similar occurrence of free carbon monoxide.

7. The percentage of free carbon monoxide which occurs in the floater of *Nereocystis Luetkeana* is considered to be a respiration product for the following reasons. It forms only when oxygen is present within the floater; it forms as readily in the dark as in the light; it is not formed by enzyme or fermentation process when the substance of the plant undergoes autolysis and decay; and it is not formed in killed plants.

In conclusion, the authors wish to acknowledge the many courtesies extended to them by Dr. T. C. FRYE, Director of the Puget Sound Marine Station.

EVANSTON, ILL.

BRIEFER ARTICLES

JAMES M. MACOUN

(WITH PORTRAIT)

JAMES M. MACOUN died on January 8, 1920, in Ottawa, Canada. During the previous summer, while exploring Jasper Park and adjoining territory in British Columbia, he was taken ill, and on his return to Ottawa in the fall his condition gradually became worse, until the end came. Being an excellent man and an accomplished naturalist his death will be mourned far beyond the confines of this continent, for Mr. MACOUN was an exceptionally active man, who kept in constant touch with learned men and institutions nearly all over the world. His career covers a great field. He was born in Brockville in 1862, and when his father, Professor JOHN MACOUN, took charge of the botanical and zoölogical work of the Geological Survey, JAMES MACOUN became his assistant in 1883.

From the time he entered the service, MACOUN specialized in botany, and in addition to other duties assisted Professor JOHN MACOUN in the preparation and publication of over 1200 pages of botanical work, and two editions of an annotated list of the birds of the Dominion. He was appointed Assistant Naturalist in 1898, and Botanist in 1917. Since 1911, when his father moved to British Columbia, much greater responsibility was thrown on him. In 1918, because of his wide knowledge in the different branches of natural history, he was appointed Chief of the

Biological Division to the Geological Survey, and was looking forward to a wider field of public service.

MACOUN's great ability to do work of a special nature satisfactorily was early recognized in the Geological Survey, and in 1891, when it became necessary to investigate the fur seal fisheries of the Pacific Islands on behalf of Great Britain and Canada, he was chosen by Dr. G. M. DAWSON, then Director of the Geological Survey and Bering Sea Commissioner for Canada, to go with him. His services in the study of the habits and life history of the fur seal proved so valuable that he was retained on this special work in 1892 and 1893, and was sent to Europe as an expert in connection with the fur seal arbitration. In 1896 he was again sent to Bering Sea, and again in 1914. In 1911 he spent 10 weeks in Washington as one of Canada's representatives at the fur seal conference. Because of this special international work he was very highly commended by Lord BRYCE, then British Ambassador at Washington, and received a C.M.G. for his services.

The field work of the staff of the Geological Survey takes the members to many parts of Canada, and mainly to the outlying, or least civilized parts of the Dominion, and during the 36 years of service MACOUN had his full share, enduring in some of the expeditions very severe hardships. As an example it will be remembered that in 1910, while studying the flora and fauna of the west coast of Hudson Bay, the ship which carried him and his party was wrecked, and they had to attempt the return to civilization in a small boat; but fortunately they were rescued and taken to Fort Churchill, from which point the party made the overland trip to Lake Winnipeg on foot, in the depth of winter, reaching the telegraph line after having been almost given up for lost.

As an evidence of the splendid work done by himself and his father, there are now in the possession of the National Herbarium of the Geological Survey, over 100,000 specimens of the flora of Canada. In addition, both men may be named among the founders of the Royal Victoria Museum of Canada, and perhaps half of the bird specimens, numbering about 14,000 in all, were supplied by the MACOUNS.

As a botanist, MACOUN proved himself a keen observer, and the enormous collections which he brought home from his expeditions contain a most excellent foundation for the knowledge of the Canadian flora. He discovered many new species, and his talent to select and prepare specimens so as to represent the variation of a number of plants was unsurpassed. Although he was more familar with the Canadian flora than any other botanist, he contributed but very little in print.

It was always his hope to be able to work up his collections sometime, but not until he had managed to acquire the literature necessary. The botanical library at Ottawa was not sufficiently provided with books in his line of work, and he was too conscientious to publish for the mere sake of publishing. It was a matter of small importance to MACOUN to make new species, he rather disliked it; he took more interest in contributing to the geographical distribution of plants, and his collections in this respect are, to say the least, invaluable. He took great interest in the difficult genus *Carex*, and he knew all the Canadian species at almost any stage of development, indeed all the varieties and forms. We owe to MACOUN the rediscovery of *Carex Franklini* and *C. petricosa*. As a botanical correspondent MACOUN was indefatigable, and one must remember that as Chief of the Biological Division he had to attend to a great amount of routine work.

In private life MACOUN took a deep interest in all questions bearing upon the progress of humanity. He took a keen and active interest in labor and sociological questions, and of late was specially interested in the returned soldier problem. MACOUN made and left many friends, and not the fewest of those who will miss him most are among the great class known as "labor." His death is a severe loss to natural science, and wherever records are given of the progress of natural science in Canada his name will be remembered, for he was one of its founders. His simple mode of life well corresponded with his sincerity as a friend, and his never failing sympathy for the poor.—THEO. HOLM, *Clinton, Md.*

CURRENT LITERATURE

NOTES FOR STUDENTS

Light and growth.—BAKHUIJZEN[1] gives a theoretical discussion of the possibility of photo-growth response as the basis of phototropic reaction. He accepts BLAAUW'S[2] view that the effect of light on the longitudinal growth is the basis of phototropic response, which is the resultant of the effect of unilateral light on the growth of the two flanks of the plant organ. This is DE CONDALLIS' old theory of phototropic response. He calculates VOGT'S data on the *Avena* coleoptile, which he believes confirms this view. From this work he believes that the retarding effect of a given dosage of light accounts for the phototropic response, and that the later accelerating effect is not involved. He finds that the effect of omnilateral fore-illumination on later phototropic response to unilateral illumination can be explained by the joint effect of the two kinds of illumination upon the growth of the two flanks, and that there is no necessity of assuming that omnilateral illumination changes the sensitiveness of the organ. This agrees more nearly with ARISZ' interpretation of his results, and is quite opposite to the view of BREMEKAMP. CLARK'S results, in which he found that omnilateral fore-illumination increased the sensitiveness of the organ in negative phototropic response, can be similarly explained. The time during which the light is applied, as well as the total energy, is important, and this will explain the results obtained by unilateral illuminations followed by omnilateral illuminations on the photo-growth basis.

LAURENS and HOOKER,[3] working on *Volvox* with various ray lengths of equal energy value, find that wave length λ 494 $\mu\mu$ has the highest stimulative value, and that the efficiency decreases with both shorter and longer wave lengths. The measurements were made both on the basis of relative duration of the presentation time and the relative rate of locomotion (and precision of orientation). Other authors have found the optimum for photo-perception and photo-growth response for various forms in this general region of the spectrum.

GUTTENBURG[4] has shown by several methods that in the coleoptile of *Avena sativa* the total plane of unilateral illumination is quite as important in

[1] BAKHUIJZEN, H. L., VAN DE SANDE, Photo-growth reaction and disposition to light in *Avena sativa*. Konin. Akad. Weten. Amster. **22**:1–16. 1919.

[2] BOT. GAZ. **59**:67–68. 1915.

[3] LAURENS, H., and HOOKER, H. D., JR., Studies on the relative physiological value of spectral light. II. The sensibility of *Volvox* to wave-lengths of equal energy content. Jour. Exp. Zool. **30**:345–368. 1920.

[4] GUTTENBURG, H. V., Untersuchungen über den Phototropismus der Pflanzen. I. Über die Abhängigkeit der phototropen Erscheinungen von der Grösse der Beleuchteten Flache. Ber. Bot. Gesells. **37**:299–304. 1919.

determining photo-presentation as the light intensity or the duration of light exposure.

GUTTENBURG[5] has also worked on the question of whether it is the direction of the ray or the relative intensity of the light on the two flanks of the plant organ that determines the phototropic orientation. His evidence points to the former as the determining factor. It is doubtful, however, whether his methods are to be compared in reliability with those of MAST,[6] which seem to prove the intensity theory.

SCHANZ[7] has just published a striking article on the effect of light of different ray lengths on the development of plants. This is one of the very rare articles that makes a really large contribution to the subject. This is assuming, of course, that his results and conclusions will be confirmed by later work. The plants were grown in beds covered with glass of various kinds that cut out different regions of the spectrum. The nine beds received the following light: (I) without cover, ray lengths λ 300 $\mu\mu$ and longer; (II) covered with ordinary window glass, ray lengths λ 320 $\mu\mu$ and longer; (III) euphos (*a*) glass only, ray lengths λ 380 $\mu\mu$ and longer; (IV) euphos (*b*) glass only, ray lengths λ 420 $\mu\mu$ and longer; (V) red glass only, ray lengths λ 560 $\mu\mu$ and longer. By combining yellow, green, and blue violet glass with euphos glass he got yellow, green, and blue violet lights respectively that were free from most of the ultra violet rays. He numbered the yellow VI, the green VII, and the blue violet VIII.

Cucumbers grown in these beds showed a rather rapid increase in rate of growth and vigor as one passed from bed I to bed V; that is, as more and more of the ultra violet and other short rays were removed. From bed V to VIII the rate of growth and vigor fell off. The curve representing the growth rate in the various beds was a mathematical curve with the peak at V. *Petunia*, *Fuchsia*, *Chrysanthemum*, *Lobelia*, *Begonia*, and *Oxalis esculenta* showed similar curves. In fact, practically all of the plants studied showed similar behavior in the rising part of the curve (beds I to V), but several showed irregularities in the falling part of the curve (beds VI to VIII). The potato was weakest in yellow, stronger in green, and still stronger in blue violet. In green lettuce the leaves became continuously longer and more slender as one passed from beds I to V. They were very slender in red, and there was a misproportion between midrib and flat portion of the leaf. In yellow the disturbance was still greater and the plants showed poor chlorophyll development. In green these plants showed similar but less marked dis-

[5] GUTTENBURG, H. V., Untersuchungen über den Phototropismus der Pflanzen. II. Neue Versuche zur Frage nach der Art der Lichtperception. Ber. Bot. Gesells. **37**:304–310. 1919.

[6] BOT. GAZ. **51**:304–305. 1911.

[7] SCHANZ, FRITZ, Wirkungen des Lichts verschiedener Wellenlänge auf die Pflanzen. Ber. Bot. Gesells. **37**:430–442. 1919.

turbances. In blue violet they were more vigorous and deep green. In short, the green lettuce showed a deficiency in chlorophyll development in yellow and green lights. Some other irregularities appeared in certain other plants.

The blooming was earlier (green lettuce, *Fuchsia*, beans, tomatoes) as one passed from bed I to IV; that is, the euphos glass, which cut out much of the ultra violet rays, favored early blooming to a marked degree. The number of fruits increased from bed I to IV. In red, yellow, green, and blue violet the blooming was deferred and the number of fruits reduced.

The ultra violet rays have a very important relation to anthocyanin development in the epidermal layer. In red-leaved lettuce the red color fell as one passed from bed I to bed III where no red developed. No anthocyanin developed in beds IV to VIII. *Celosia Thomsoni*, red-leaved begonia, and red-leaved beet acted similarly, except that anthocyanin developed in the midribs and petioles of the last in all the beds. When any of these plants were grown in beds where anthocyanin did not develop, and were then transferred to bed I, anthocyanin began to appear in 2 days and was fully developed in 8 days. When plants grown in bed I and bearing anthocyanin were transferred to beds III to VIII, the new leaves unfolding in the latter beds were without anthocyanin.

In all plants except one SCHANZ found no evidence that the red pigment functioned in protecting the plant against the injurious action of the ultra violet of the solar spectrum; for when plants were transferred from bed IV, where no red pigment developed, to bed I, no injury appeared, but the leaves soon developed the pigment. Red beech was the exception. When this plant was transferred from bed IV to bed I, the old leaves without pigment died within a few days, and the new leaves unfolding developed the red pigment.

The rate and percentage of germination of seeds (lettuce and stinging nettle) increased from bed I to bed IV. Repeated cultures on these forms showed that ultra violet interferes with germination.

When etiolated seedlings (bush beans, soy beans, potatoes) were transferred to the beds, the order of greening, beginning with the fastest, was red, euphos *b*, euphos *a*, ordinary glass, open bed, yellow, green, blue violet. The development of chlorophyll is favored by a greater and greater removal of the ultra violet. Also chlorophyll decomposition is deferred in old plants by screening out the ultra violet rays.

SCHANZ mentions the fact that in Holland many growers prefer crude glass to regular window glass for forcing houses. He finds that crude glass cuts out more of all rays than window glass, but that it is especially effective in screening out ultra violet, and concludes that any possible detrimental effect from reducing light intensity for synthesis is more than counteracted by the benefits derived from screening out injurious ultra violet rays.

From these results it seems evident that SCHANZ was fully justified in his earlier statement that ultra violet light of the solar spectrum has a remarkable effect on the development of plants.

In his very extensive work KLEBS has always maintained that the action of red light was due to the fact that it has high photosynthetic action. SCHANZ's work suggests that the effect may be due in part to the fact that it eliminates detrimental ultra violet rays.

This very important work of SCHANZ merits checking up and extending. The work with ultra violet light has been largely with artificial spectra much richer in ultra violet than the solar spectrum, and too little exact study has been made of the formative effects of the ultra violet of the latter spectrum.

A very noteworthy piece of work by GARNER and ALLARD,[8] reviewed in detail elsewhere in this journal, should be mentioned in this connection. It is possible that the remarkable effects they obtain from length of day is due to the fact that it modifies the nitrogen *carbohydrate* ratio of which FISCHER, KRAUS and KRAYBILL,[9] and others have made so much as a determiner of the course of development, whether vegetation shall dominate or there shall be a balance of vegetation and reproduction.

In the small dosages of light used in phototropic and photo-growth response, the most effective region of the spectrum on the basis of equal energy value lies at λ 505 $\mu\mu$ for the sporangiophore of *Phycomyces;* at λ 467 $\mu\mu$ for the coleoptile of *Avena;* and at λ 494 $\mu\mu$ for *Volvox*, as previously given. Perhaps with the high dosage of natural illumination the effective region shifts still more to the right as is indicated by SCHANZ's work.

A comprehensive study of the formative effect of light on plants is much needed to see to what degree its formative action is due to synthetic activity, to the so-called photo-growth responses, to various effects of ultra violet rays, and to other effects not included in these.—WM. CROCKER.

Effect of light exposure on plant growth.—GARNER and ALLARD[10] have grown plants under different conditions of light exposure, and have made a special study of the tendency to become reproductive or to remain vegetative under varying daily lengths and intensities of exposure. Several varieties of tobacco and soy bean were mainly used in the experimental work, although numerous other species of annuals and biennials were used to check the results attained.

Plants were grown in pots, buckets, or boxes, and at the desired time each day were moved into dark chambers which were placed in the field. For the last season's work, large dark houses were constructed, in such a way that plants could be moved in or out at any time. Time of exposure to light

[8] GARNER, W. W., and ALLARD, H.A., Effect of relative length of day and night and other factors of the environment on growth and reproduction in plants. Jour. Agric. Res. **18**:553–606. 1920.

[9] BOT. GAZ. **67**:445–446. 1919.

[10] GARNER, W.W., and ALLARD, H. A., Effect of relative length of day and night and other factors of the environment on growth and reproduction in plants. Jour. Agric. Res. **18**:553–606. 1920.

varied in the different tests from 5 hours daily to full daylight, 7 and 12 hours being the exposures chiefly used. Checks received full daylight under similar conditions of temperature. Shorter light exposures were all made during the middle of the day, and during the time of highest light intensity, except one series of soy beans which were kept in darkness from 10:00 A.M. to 2:00 P.M. daily.

In general, the amount of vegetative growth was proportional to the length of daily exposure to light. The short exposures resulted in short, slender plants of greatly reduced size. Rate of growth was much slower, and the total size attained was reduced. The inception of the flowering or reproductive phase was greatly influenced by length of exposure to light. Many of the species worked with were thrown into flowering and fruiting by the shorter exposures, while with certain other species and varieties, reducing the period of illumination had little effect upon the inception of fruiting.

The authors conclude that for each plant there is a "critical" length of daylight exposure essential to the development of the fruiting phase. The length of this critical exposure varies with each species and variety, but, in many individuals at least, is very much shorter than normal summer daylight. By exposing the plants to this critical length of illumination, the reproductive or flowering phase can be induced at almost any time. By varying this time of exposure, typical biennials, as *Aster linariifolius*, could be made to complete their life cycles within a few months, while annuals, as soy beans, *Solidago*, etc., could be induced to respond as biennials.

Experiments with shading indicated that time of exposure, and not light intensity, is the primary factor involved in determining the critical day. Light intensity reduced to 43 per cent by shading had no effect upon the time of inception of fruiting, although it did give typical shading results on form and amount of growth. Of significance, however, is the result obtained from exposing soy bean morning and afternoon, but keeping it in darkness during midday. Time of fruiting was not materially altered by this treatment, although it was much advanced in the same variety by reducing the exposure to light through leaving in darkness morning and evening. Reducing the water supply reduced vegetative growth and fruit yield, but did not alter time of fruiting in the least. Winter light, supplemented by artificial illumination at night, giving a total daily exposure of 18 hours, acted exactly as long summer daylight in its tendency to retard or prevent fruiting. The authors believe length of day, through its influence on fruiting and seed formation, to be a fundamental factor in plant distribution.

No attempt has been made by the authors to explain how length of day might thus determine the form of plant development. It is unfortunate that a more careful review of the literature was not given, as the authors have made no attempt to link their work to other very critical studies along this line. KLEBS found that by varying the salt nutrients, he could induce vegetative or reproductive growth at will, over a very wide range of plants.

He found high salt supply gives vegetative growth, while low salt supply induces fruiting. FISCHER found that increasing photosynthesis and the supply of carbohydrate material, through increased CO_2 pressure, the nitrogen supply remaining constant, induces the reproductive phase. Finally, in a series of very critical experiments and analyses, KRAUS and KRAYBILL found that a relative abundance of carbohydrate over nitrogenous material in the plant induces fruitfulness, while a relatively greater nitrogen supply induces vegetative growth. Excessive carbohydrate over nitrogen inhibited both vegetative and reproductive growth. All of this work shows a very close relation between the conditions of nutrition in the plant and the type of growth expression. GARNER and ALLARD have undoubtedly made a contribution of great value to the subject of vegetation and reproduction in plants. The reviewer feels, however, that their conclusions are much broader than a careful review of the whole subject warrants. It would be difficult, for example, to explain the phenomenon of alternate fruiting in many of our orchards on the basis of length of day influence. A critical study of the nitrogen and carbohydrate metabolism under these reduced exposures to illumination would be of great value in arriving at an understanding of the many factors in plant growth and reproduction.—J. R. MAGNESS.

Ecological research.—In a report of research in progress under the direction of the Carnegie Institution, Director MACDOUGAL[11] reports progress upon a number of interesting problems. SHREVE has continued investigations upon the vegetation of the arid Avra Valley, and reports progress in a soil temperature survey of the United States and Canada. CANNON presents some conclusions derived from a field study of the vegetation of central, northern, and southwestern South Australia, as well as some further results in the investigations of the reactions of roots to varying amounts of carbon dioxide in the soil. He has also some data as to the size and form of leaves of desert plants. COOPER reports the beginnings of a study of the strand vegetation of the Pacific Coast at Coronado and Monterey, California. These regions possess interesting dune areas, upon which various plant associations, varying from pioneer herbaceous to chaparral and forest communities, have become established. These communities are being mapped, permanent quadrats and transects established, and the underground portions of many species excavated and studied. Measurements of evaporation, soil moisture, and soil temperature have been made, and material collected for anatomical studies. MACDOUGAL and SPOEHR are conducting investigations to discover the origin of xerophytism in plants, and Mrs. SHREVE has records extending over several years of seasonal changes in the water relations of such desert plants as *Encelia farinosa*, *Streptanthus arizonicus*, and *Amaranthus Palmeri*.—GEO. D. FULLER.

[11] MACDOUGAL, D. T., Ecology. Carnegie Inst. Wash. Year Book for 1919. **18**:87–102. 1920.